

A MANUAL OF
ELEMENTARY ZOOLOGY

A MANUAL OF ELEMENTARY ZOOLOGY

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PREFACE

IN the following pages I have endeavoured so to treat of the animals which are most often studied in courses of Elementary Zoology as to introduce the student by their means to the principal problems of the science. I have tried at the same time not to state facts in terms of any theory, but to expound theories after the facts upon which they are based. I have assumed that the student will have an elementary knowledge of Chemistry and Physics.

One general principle has guided me—that the organism should be regarded as a whole. Thus I have not adopted views which ascribe to certain morphological constituents of the body of an organism, such as cells and zooids, a mystical “individuality,” based upon assumptions with regard to their history or potential independence. I have taken indivision, not indivisibility, to be the essence of individuality.

My very sincere thanks are due to a number of gentlemen for assistance of various kinds. Professor J. Stanley Gardiner has been kind enough to read almost the whole of the work, and has given me invaluable advice. Mr. J. Barcroft, Mr. H. H. Brindley, Mr. C. Clifford Dobell, Mr. L. Doncaster, Dr. H. Gadow, Professor E. W. MacBride, and Professor R. C. Punnett have each seen portions of the book, and I am greatly indebted to each.

of them for suggestions. In dealing with the cell theory, I have made use of the illuminating contrast drawn by Mr. Dobell between the Protozoa as non-cellular animals and the Metazoa as cellular. I am under great obligations to my artists, and in particular to Mr. J. K. Maxwell, Mr. Edwin Wilson, and Mr. M. P. Parker, by whom the majority of the drawings were made. Professor J. Arthur Thomson has kindly consented to my borrowing from his *Outlines of Zoology* a large number of illustrations which are the property of the publishers of this work. Messrs. Bell & Sons, Messrs. Kegan Paul, Trench, Trübner, & Co., and the Cambridge University Press have permitted me to reproduce illustrations from works owned by them. My acknowledgments to the authors of these works are made in the legends of the figures.

L. A. BORRADILLE.

SELWYN COLLEGE, CAMBRIDGE,
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ERRATA

- Page 84, line 2 of footnote, *for* "nucleins" *read* "nucleins."
- Page 97, line 5, *for* "flat" *read* "thin."
- Page 181, line 11, *for* "108" *read* "109."
- Page 183, fig. 111 is from Thomson.
- Page 186, line 3, *for* "the parasitic maggots" *read* "parasitic maggots which are the young of."
- Page 207, line 18, *for* "pleura" *read* "pleuron."
- Page 226, line 23, *for* "limbs of the first two segments" *read* "antennules and antennæ."
- Page 226, line 25, *after* "which" *insert* "as a result of cephalisation to a high degree (p. 204)."
- Page 231, legend of fig. 145, *for* "from the side" *read* "in section."
- Page 233, line 26, *for* "Insects" *read* "Crustaceans (water-fleas, crayfish, etc.), insects."
- Page 238, legend of fig. 151, *for* "tarsu" *read* "tarsus."
- Page 316, line 2, *for* "upstroke" *read* "downstroke."
- Page 326, fig. 225, *for* "hm" *read* "thm."
- Page 369, legend of fig. 253, *after* "of" *insert* "the fin-whale."
- Page 392, fig. 276B, the line from "n.f." should run more to the right.
- Page 441, line 15, *for* "any" *read* "many."
- Page 442, line 4, *omit* "of quicksilver."
- Page 458, line 32, *for* "Cephalochorda" *read* "Cephalochorda."
- Page 468, line 17, *after* "efferent" *insert* "branchial."

A MANUAL OF ELEMENTARY ZOOLOGY

CHAPTER I

INTRODUCTORY: THE ANIMAL ORGANISM

NOTHING is of more importance to the student of Zoology than to realise at the outset of his studies what **The Subject.** is the scope of his science. Zoology is concerned with animals. Now it is quite possible to regard animals merely as objects of certain shapes and sizes and colours, and to study and classify them with reference to these properties alone. But this procedure is both unintelligent and unfruitful. It ignores the meaning of the facts which it collects, and leaves unanswered the questions which they suggest. Properly to study any animal we must inquire why its structure is what we find it to be, and how it has come into being. That is to say, we must study, with the structure of the body, the life which that structure subserves and to which it owes its existence, for the life of an animal not only requires in it a certain structure, but is also the means by which that structure is reached both in the individual and in the race.

Life. The life of an animal consists in a series of processes which take place in its body. So long as these processes go on the animal is said to be alive; when the body has lost the capacity for supporting them it is dead. In their main outlines the processes of life are familiar to every one in his own person, and in those of the men and animals about him. They may be stated as follows.

The body of a living man is always at work. In moving, in producing the heat which usually keeps him warmer than the air around him, in the manufacture of such liquids as sweat, spittle, and tears, in the activity of the brain which is known to accompany thinking, in a thousand ways this is seen from moment to moment of his life. Even in sleep the heart-beat and breathing go on. Now this, like all other work, involves the using of energy, and the energy of the living body is not imparted from without, as the energy which causes a kettle to boil is imparted by the fire, but derived from within, as the energy which drives the shot from a gun is derived from the explosion of the powder within it, or a steam-engine, regarded as a whole, obtains its energy from an internal furnace. If, however, the body is to evolve energy from itself, it can only obtain that energy by some rearrangement of the particles which compose its own substance. Nor is it necessary to look far for evidence of the occurrence of such a process or for information as to its nature. Let us consider for a moment the way in which the energy of the work of a steam-engine is obtained. It depends upon the fact that whenever atoms unite to form molecules energy is set free, and the stabler the molecules formed the greater, almost invariably, is the amount of energy liberated in their formation. The same amount of energy must be used to break up a molecule as was set free when it was formed. The substances which are used as fuel consist of molecules which are complex and relatively unstable, and rich in energy. The furnace of the engine, receiving constantly and often under forced draught fresh supplies of air, breaks down the molecules of its fuel and unites the carbon and hydrogen atoms of which they principally consist with the atoms of the oxygen in the air, to form smaller and more stable molecules of carbon dioxide and water. This process is, of course, the burning of the fuel. The energy freed in the formation of the stable molecules is so much greater than that which is required to break down the unstable molecules that a large balance of energy is freed and becomes available for driving the engine. The chemical energy of the fuel and the oxygen becomes trans-

The Life Processes : I. Disintegration with (a) Evolution of Energy.

formed, after several changes which do not concern us, into the energy of the mechanical work of the engine. Regarded as a whole, the process is a destruction or disintegration of certain substances, with the liberation of a large part of the energy which they contain. Now it may be shown that the body receives by forced draught in breathing constant supplies of oxygen, burns the complex, unstable molecules of its substance, and obtains thus the energy for its actions,¹ discharging as waste in the breath, urine, and sweat the simpler substances that it has formed. In short, the substance of the body is constantly undergoing *disintegration with evolution of energy*.

It is not difficult to prove that this process is taking place. Since the molecules of the body substance contain, like those of the fuel of the engine, large quantities of carbon and hydrogen, together with some oxygen and nitrogen, the products of their disintegration include carbon dioxide, water, and certain relatively simple compounds of nitrogen, such as urea, $\text{CO}(\text{NH}_2)_2$. The intake of oxygen and loss of carbon dioxide during life are easily demonstrated. Men or animals enclosed in a vessel to which air has not access are unable to live for more than a short time. The animals are stifled, just as a fire or the flame of a candle may be stifled by want of air, and subsequent examination of the gases in the vessel will show that the oxygen has been depleted and replaced by carbon dioxide just as it would be if a candle had been burnt in it. This exchange with their surroundings of carbon dioxide for oxygen is characteristic of living animals and is known as *respiration*. In man and animals like him it takes place through the lungs, in breathing. If the breath be tested, it will be found to have undergone the same changes as the air in a vessel in which an animal has been stifled. Fishes and other aquatic animals use the oxygen which is held in solution in the water in which they live. The nitrogenous

¹ The analogy between the living body and a steam engine must not be pushed too far. It is not at all certain either (a) that the body is a heat engine like the steam engine, or (b) that the oxidation takes place in the same way in the two cases. It is very possible that the oxygen which is taken in is first built into complex molecules of the body substance, by whose subsequent breakdown the energy of the life processes is obtained.

waste matters may be identified in the urine by chemical analysis. The formation of water is less easily demonstrated, because the bulk of the water lost to the body has been taken in as such through the mouth in order to perform certain indispensable functions, one of which is the washing out of the nitrogenous waste, but a careful comparison of the quantities of water which enter and leave the body shows that more goes out than can be accounted for by what has entered.

The energy freed in the disintegration of the body-substance appears, as we have seen, in various ways. The most characteristic and important of these are contraction, chemical work, excretion, secretion, and possibly the conduction of impulses. *Contraction* is the process by which mechanical movements are carried out. In it a portion of the living substance changes in shape but not in size, growing shorter in one direction but wider in others. This may easily be felt in the working of any of the great muscles of the human body, as when the well-known "biceps," in shortening to pull up the forearm, grows at the same time wider. Instances of *chemical activity* are seen in the formation of the constituents of the many juices which are used for various purposes in the body. Thus the "gastric juice," by which food is digested and disinfected in the stomach, contains among other substances hydrochloric acid, whose formation in face of the alkalinity of the blood involves very considerable chemical work. Other examples of liquids formed for special purposes are the spittle or saliva which helps in the swallowing of food, tears which wash clean the surface of the eyes, and so forth. The regions in which materials are thus formed are known as *glands*. Lastly, a part of the energy liberated in the body is used in the removal from the substance of the body of the chemical products of its activity. We have seen that in the process of disintegration there arise waste products of which the body gets rid. We have just seen also that certain of its actions consist in the chemical manufacture of materials which are not purely waste but have their uses to the body. The casting out from the substance of the glands of the materials formed in these two cases, and of

(b) Appearance of the liberated Energy in various forms.

the water in which they are dissolved, is a necessary part of the working of the bodily machine. The waste products are got rid of because they are poisonous, and the products of chemical manufacture are removed in order to be of use elsewhere. Both kinds of material are accordingly shed, sometimes upon the surface of the body, but usually into vessels which conduct them to the required locality. This shedding out is a distinct process, carried on by an exercise of the activity of the living substance of the body. No real distinction can be drawn between the two cases, but the process is called *excretion* when the substances cast out are purely waste, as in the urine, and *secretion*¹ when they are of some further use to the body, as in the gastric juice. Finally, it is possible that an expenditure of energy is involved in the conveyance of the impulse which starts any response from the spot where the stimulus is received to the locality where the main part of the response takes place. Thus, when a drop of water which has fallen upon the skin is brushed off, an impulse is started in the skin and conveyed along those tracts of the body which we know as nerves till it causes such movements of the muscles of the arms as are necessary to brush off the drop. This property in living matter of conveying impulses is known as *conductivity*. The mode of conduction is not understood, but it may be that it involves the evolution of energy by the disintegration of the conducting substance.

It should be noted that the forms in which the energy of the body is used in these various processes are very different. Besides mechanical movement, the exhibition of *molar* energy, it may bring about *chemical* changes, or become *heat*, as is shown by its warming the human body, or *light*, as in the glow-worm, or *electricity*,² as in the well-known electric eel; and there are other processes, such as secretion, in which its action has not yet been certainly compared with any event in the lifeless world and is sometimes supposed to be of a kind peculiar to the

¹ The term "secretion" is sometimes loosely used to include the formation as well as the removal of chemical products, or even applied to the substances secreted.

² Small electrical changes accompany many of the processes of the body.

living body. We shall return to this question in a later chapter.

It is thus characteristic of the living body to be continually wasting away by disintegration. Clearly this could not go on indefinitely without some compensating repair. The waste is made good by the *incorporation* of food. Two

II. Incorporation of Food:

(a) **Absorption.** Two distinct processes may be recognised in incorporation—absorption and assimilation. Before it can be absorbed the food has generally to undergo a preliminary process of *digestion*, whereby the solid or indiffusible nutriment which it contains is made soluble and diffusible. The food of all animals must contain the following materials: (1) *water*, (2) certain *inorganic salts*, such as the chlorides and phosphates of sodium, potassium, and calcium, (3) the very complex compounds known as *proteins*. A protein is a colloid substance consisting of carbon, hydrogen, nitrogen, and oxygen, with small quantities of sulphur and sometimes phosphorus. A familiar example is the “albumen” which, mixed with water, forms white of egg. The molecular structure of proteins is not yet fully understood,¹ and they have not yet been made in the laboratory. Besides these substances the food usually contains (4) *carbohydrates* (sugars, starches, and related substances), (5) *fats*. Proteins, carbohydrates, and fats belong to the class of compounds known as “organic,” which, in nature, are found only in the bodies of plants and animals and in their remains; all animals therefore require for food the bodies of plants or of other animals. The digested materials undergo *absorption* into the substance of the body, leaving the indigestible matter to be cast away as the *dung or feces*.

Incorporation, however, is not brought about simply by the absorption of digested matter. The food, after as before digestion, is not of the same composition as the substance to which it is to be added. The flesh of a dead ox or sheep differs considerably in composition from that of a living man, and the difference is increased by its digestion. In the course of incorporation the food has therefore to undergo

(b) Assimilation.

¹ They are probably exceedingly complex linkages of amino-acids.

chemical changes by which it is converted into the substances which compose the body, and these changes it undergoes by the activity of the living matter itself. That is to say, the living substance has the power of making, out of unlike materials, additional matter of its own composition. The process by which this is done is known as *assimilation*.

The incorporation of new material has a further effect than the mere *repair* of the waste caused by disintegration. Throughout the body of a young animal, and in such parts as the roots of the hair and nails even in age, incorporation takes place in excess of waste, so that *growth* occurs. Both in repair and in growth the new material is not added in layers to a surface, like that which is taken up by a crystal, but is placed between the existing particles, as a substance is taken into solution. Growth, moreover, is a very complex architectural process in which the intricate structure of the body is built up out of many materials. The meaning of the growth of the body will be better understood when we have studied reproduction.

It will be seen that disintegration and its complementary *assimilation* constitute a series of chemical changes, continually taking place in the body, whereby there is kept up a continual evolution of energy. These changes, regarded as a whole, are known as *metabolism*, the disintegrative changes being known as *katabolism* and the assimilative as *anabolism*.

The outward expression of the incorporation of food is to be found, as we have seen, in growth. Now growth is followed, sooner or later, by *reproduction*. That is to say, a portion of the body breaks off to form a new individual which leads an independent existence. It will be convenient to use the word "fission" to denote the actual breaking away of the new body, for reproduction is more than a mere act of separation. This will be seen if we consider it a little more closely.

(a) As has been said, *reproduction always involves the fission of an existing body*. Life never arises anew, but is always passed on from one living being to another which

arises from it. A living being which divides to produce others is a *parent*, those which it forms are *offspring*.

(b) *The offspring are always at first unlike the parent*. There are, as we shall see, certain animals in which the only evident difference between the offspring and the individual by whose division they arose is the necessary one of size. But in the great majority of cases there is also an obvious difference in form, the offspring being at first very unlike the parent in structure. This difference is obscured in the case of man and some other animals, where

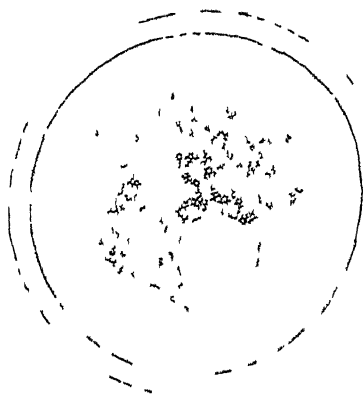


FIG. 1.—The egg or “ovum” from which a human being is developed, highly magnified.

the offspring undergoes changes in the womb before birth (Fig. 1), but it is seen unmistakably in animals which are born in the condition of an egg. In their immature condition the offspring are known as *reproductive bodies*.

(c) In spite of this unlikeness at starting, *the offspring become in time like the parent from which they arose*, owing to a succession of changes which is sometimes direct, sometimes, as in the

well-known case of the butterfly, very indirect. Thus the life of an animal is a *cycle*, in which it passes through a series of stages, beginning with the small and simple reproductive body, and ending with the larger and usually more complex *adult*, ready to undergo fission again. Every individual goes through the same cycle of changes as its parent, resembling in each stage a similar stage passed through by the latter, till it reaches the likeness of the individual that produced it. This is due to the property known as *heredity*. In a later chapter we shall have occasion to examine heredity more closely.

It will be seen that, in the strict sense of the word, reproduction includes the whole life cycle, and consists of two distinct processes—*fission*, and the *development* of the reproductive body into the adult—for until this cycle has been completed the parent is not re produced¹

The meaning of *growth* will now be apparent. It is that part of the process of development by which the reproductive body reaches the size of the adult. At the same time, in most cases, and perhaps in all, the growing individual is undergoing the *changes in structure* to which we have alluded.

Here must be mentioned a process which it will not be possible properly to discuss till some examples of it have been studied in detail. It

is well known that in most animals reproduction is only possible by the co operation of two individuals of different kinds known as the *sexes*. This is because in such animals the reproductive bodies are of two sorts, each produced only by one of the sexes, and neither sort can develop except after fusion with one of the other sort. That fusion is an example of the process known as *conjugation*. From time to time there occurs in nearly all animals such a union of two distinct portions of living matter. The bodies which unite are known as *gametes* and that which results from their fusion as a *zygote*. In large and complex animals conjugation takes place only between the reproductive bodies, which are generally unable to develop without it, so that, as we have seen, it becomes a part of the reproductive process. In these cases the reproductive bodies are of a kind known as *germs*, distinguished from other reproductive bodies by their small size and the simplicity of their structure. The germs of such animals are, as has been

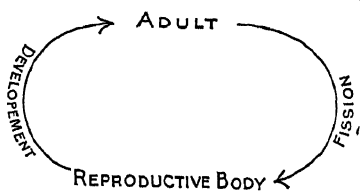


FIG. 2 —A diagram of the life cycle of an animal

¹ Development may partly take place before fission, as in many cases of budding (Chap. X.)

said, of two sorts. One is larger and passive, and is known as the *egg, ovum, or female gamete*. The other is smaller and active, and known as the *spermatozoon or male gamete*; it

moves to the egg and enters it, and is then said to *fertilise* it. Ova and spermatozoa are usually formed by different adults, known respectively as *female* and *male*, but in some cases both kinds are formed by one individual, which is then known as a *hermaphrodite*. In some aquatic animals the gametes are set free, and conjugation takes place outside the body of the parent. In many cases, however, the ova are kept within the body of the mother, and the male gametes, known collectively as the *sperm*, are transferred by the male to the body of the female and there seek and fertilise the ova. This transference is known as *coition*. Reproduction in which conjugation is necessary before development of the germs can take place is known as *sexual reproduction*. That in which conjugation does not take place is *asexual*. We shall see (Chap. VII.) that in some of the smallest animals conjugation takes place, not between newly formed germs, but between fully grown adults, and has thus no such connection with reproduction as is usually found.



FIG. 3 — Human spermatozoa, highly magnified, seen in face and in side view.—After various authors.

Direction of the Life Processes:

The statements that have just been made deal for the most part with facts that are quite well known, and cover all the activities of animals; yet they do not give a complete picture of life, for they do not take into account the meaning of the processes in which it consists. They

give no information as to why these processes take place and what are their results. The characters that we have so far considered in living animals are processes that take place in their bodies. We have now to note certain

characters that concern rather the direction of these processes

The most striking characteristic of a living animal is that it *responds to stimuli*. We can see this very clearly in considering our own lives. The coming into sight of an enemy or a friend, of food or some other coveted object, or of printed words, the sound of the movement of wild animals, of an entreaty or a command, or of music, the approach of some substance which can be smelt, the falling of a blow—such changes in his surroundings as these constitute stimuli to which a man, as we know, responds either by doing something which he had not been doing before or by ceasing from something which he had before been doing. That is to say, there occurs in his body a change which corresponds to the change which has taken place outside him. It is, indeed, of events which thus start, or are modified, in response to stimuli that the life of man is made up. From the first feeble cry that is drawn from his little body by some discomfort in the world of chequered experience into which he has been born, response is the most easily recognised feature of his life until that hour when his dead lips fail to answer his friends. The capacity for receiving stimuli which start or stop in the body an activity of its own is known as *irritability*. Two things must be noted concerning the internal changes in which such activity consists. Firstly, that their energy is derived, as we have seen, not from without, as when a change is brought about in water by heating it, but from within, as when a change is brought about in gunpowder by heating it. Secondly, that the extent of the internal change bears no relation to that of the external one which acts as its stimulus. Thus when, in response to a command, a man lifts a heavy load, the energy of the sound-waves which call forth this reaction is immeasurably smaller than that of the work done by the man, and either may be greater or less without a corresponding alteration in the other.

Activity, however, is not necessarily associated with irritability. It is sometimes claimed that the activity of living animals is characterised by a feature which is in its essence the very opposite of irritability. This feature is

called *automatism*, the word meaning that certain actions of the beings of which it is used arise independently of external stimuli. Now in a certain sense it is true that this is the case. That is to say, in the living animal there do arise actions which are not the direct result of any stimulus from without. The simplest instance of this is the beating of the heart, but we are well aware that some of our more complicated actions are at least not due to any stimuli which we can trace. In view of the great number of stimuli which the body is always receiving, it is necessary to be cautious in attributing an automatic character to any of its actions, but there is little doubt that automatism, in the sense in which we have used the word, is characteristic of the living animal.¹ It must be borne in mind, however, that automatism does not consist in any action being completely independent of the outer world, since the constitution of the animal is due in part to the effect upon it of its surroundings.

The living animal has not come into being, as it could not exist, independently of its surroundings. Its whole constitution² is due, not only to the properties inherent in it when it was formed by its parent, but also to all the influences by which it is continually being affected from its first moment, some of which, such as food and a certain temperature, are essential to its existence and development, while all bring about permanent alterations in it by its own activity in responding to them. Thus the existence and peculiar features of a bird are due to the warmth which brings about its formation in the egg, as well as to those qualities in the egg which cause it to give rise to a bird; and every child, in response to the voice of its elders, learns facts and sets up habits which affect its mental constitution throughout life. It, therefore, in virtue of its constitution, there occur in the living animal actions which are not the direct result of any external stimulus, such

¹ An action is none the less automatic because it is modified by stimuli. It is well known, for instance, that the beating of the heart may be hastened or slowed by stimuli such as those which are afforded by an event which arouses great joy or fear. Nor, again, does an action cease to be automatic because it cannot be maintained unless a supply of nourishment be provided for the body in which it takes place, as the beating of the heart is dependent on the quality of the blood which nourishes it.

² The use of the word "constitution" here does not prejudice the question whether the constitution of an animal, as the biologist is concerned with it, is a purely physical thing.

actions have nevertheless not occurred independently of the influence of its surroundings, since the constitution itself is the result of a history in which that influence has played an essential part. In so far as the surroundings have a share in forming any animal, they have a share in causing its automatic actions.

We have now dealt with the way in which the life processes arise. From what has been said it will be clear that, whatever part the organism itself may play in automatism, *directly or indirectly, everything that happens in an animal is a reaction to events that have happened outside it*. But if the processes which make up life are a reaction to changes in the surroundings, they are a reaction of a very special kind. This is quite clear when disintegration within the body is compared with that which may be brought about in lifeless things. (a) When a bonfire is made the energy of the fuel is spent without accomplishing any definite end. When a fire burns in the furnace of an engine *its energy is directed* towards the working of the engine. We have seen that the expenditure of energy in the body is of this kind. (b) At the same time the result of the working of the bodily machine is different from that of the working of a lifeless engine in that it is *directed towards an end in relation to the body itself*. When a man seeks food or avoids unfavourable circumstances, when he converses with his friends or strives with his enemies, when he shapes his doings in accordance with warnings received by ear or from print, he is acting in his own interests. He may fail, but the tendency of his action is such as would in most circumstances be directly or indirectly to his benefit, even though in particular circumstances it may compass his destruction, as when the natural response to the stimulus given by the sight of things which seem to be good for food causes a child to eat the berries of the deadly nightshade¹. But no such tendency can be found in responses that take place in lifeless things. Internal action there may be or not in response to external changes, but such reaction, if it occur, is here without regard to the welfare of the body in which it takes place. A blow

¹ It is, of course, possible by unnatural stimuli to bring about quite meaningless responses, as when electric shocks cause aimless movements of the limbs. But even here the mechanism which is set in action is that which in ordinary circumstances is used for purposive movements.

given to a cartridge produces a response in the cartridge, but the response is without purpose as regards the cartridge and leads incidentally to its destruction. A blow given to a living animal produces a response which varies indeed according to circumstances but tends always, by flight or by resistance, to the avoidance of danger. Action such as this, with a tendency to the accomplishment of a definite end in relation to the acting body, is said to be *purposive*. It should be noted, however, that the use of this word does not imply that the actions in question are directed by will. The term is concerned only with the result of the action, not with the means by which it is directed to that result. Purposiveness pervades all the activities of animals. It is not confined to direct response, but is found also in automatic actions, which always tend to the benefit of the being in whose body they occur. Needless to say the incorporation of food is purposive. On the other hand, it must be recognised that reproduction, purposive though it is, is directed, not to the welfare of the individual in which it takes place, but to that of the whole species of animal to which that individual belongs. Every kind of animal is continually losing its individuals by death, and it is obvious that unless there were provided by reproduction a constant succession of new individuals the species would die out.

The consideration of reproduction in this connection shows clearly that the life processes are a unity. The purposive character of life consists not only in the tendency of each individual act, but also in the way in which *all the activities of the body are interwoven* so as to produce a single result. Each process is related to the other. The incorporation of food is in great part a preparation for disintegration. On the other hand, much of the energy set free during disintegration is spent in obtaining and making ready food for incorporation. And in the long-run all the other life processes, whether their immediate end be the avoidance of danger, the increase of the substance of the body, or any act subsidiary to either of these (such as the removal of waste), are directed to the preparation and preservation of the individual for reproduction, whereby the species is

**The Unity of
the Life
Processes.**

continued Thus all the activities of a living being combine to continue the existence of its kind

It will be seen that the two factors by which the course of the life processes of any animal is governed are (1) the constitution (p. 12) of the animal, which sets up certain "automatic" activities and permits the modification of these and the starting of certain others, (2) stimuli received from its surroundings. Now the constitution is due primarily to the tendencies with which the animal was born, but, as we have already seen, it is due also to external influences, which not only enable it to keep in existence and develop along a hereditary path, but are also continually altering it and thereby altering the behaviour of the animal. These influences are never the same in any two animals, since no two can ever live precisely the same lives. Thus, even if we suppose that two animals are born with identical constitutions, they will not remain identical. The consequence of this is that *the history of the individual animal is a factor in determining its behaviour*. The burnt child dreads the fire, the actions of an athlete are quicker and more powerful than those of an untuned man, hardship may cause permanent enfeeblement. Clearly, while the effects of the historical factor are sometimes harmful, the nature of the organism is such that in many cases they increase the efficiency of its purposive reactions.

These features in the activity of living beings place them in a relation to their surroundings which is entirely different from that of lifeless things. The forces of nature acting from without upon a lifeless object find in it a toy or a passive victim. In the living being they set in action a machine of great efficiency which reacts upon them for its own benefit. The result of this is, in the animal, ability to exist amid surroundings which would destroy it but for its life. In the world as a whole the result is a complication of the action of its forces which is a factor of enormous importance in the system of nature. By the living machine these forces bring about results which they could not otherwise accomplish. The history of this reaction is written large in the very substance of the earth. Enormous beds of chalk and limestone composed of the skeletons of minute marine animals, countless coral reefs and islands, vast areas covered with vegetable mould by the action of plants and earthworms, and great tracts of country whose face has been changed by human activity bear witness to its existence, and since the coming of Man it has progressed more and more rapidly till it promises to dominate every other terrestrial agent of change in nature.

We are now in a position to sum up the characteristic features of the complex process which is known as life. In doing so we shall arrange them in a somewhat different order from that in which they have come under our notice, stating successively those that relate to the starting of the life processes, to the nature of these processes, and to the end to which they tend. We have found in life :¹—

**Summary of
the Character-
istics of Life.**

1. The exhibition of *Irritability*—the starting or stopping in the body of an activity of its own as the result of the receipt of a stimulus.
2. *Automatism*—the starting or stopping of activity without an immediate external stimulus.
3. *Disintegration with liberation of energy*, this energy appearing in various processes, of which the most conspicuous are .
 - i. *Contraction*, or change of shape,
 - ii. *Chemical work*,
 - iii. *Excretion and Secretion*, the shedding out from the substance of the body of chemical products,
and possibly also in the *Conduction* of the impulses which start these processes from one part of the body to another.
4. *The Incorporation of food*, which involves (a) the *Absorption* of new material, (b) the conversion by *Assimilation* of unlike substances into the substance of the body.
5. *Reproduction*, which involves (a) the breaking off or *Fission* of a part of the body, and (b) the process of growth and structural change known as *Development*.
6. *Purposiveness*—the direction of the activity of the body towards its own preservation and that of its kind.

¹ We have not included in the following list the process of respiration because, though it is often rightly cited as a characteristic feature of the life of animals, it is not a simple or distinct process. It consists in the excretion of carbon dioxide and the taking up of oxygen by a process which is not in its essence different from the incorporation of other materials. We have rejected conjugation because it is not a universal property of living matter.

The relation of the life of animals to their structure is very clear in the light of what has just been said. The animal body is a machine which reacts to events in the outer world in such a way as to prolong its own existence and that of its kind. Like other machines, it consists of a number of parts each of which does a particular portion of the work of the whole. Such parts are called *organs*. Thus there are *sense organs*, such as the eyes and ears, for the reception of stimuli, *nervous organs* for the conduction of impulses, set up by these stimuli to the organs which carry out the main part of the reaction, *locomotive organs*, such as legs, and wings, and fins, to carry the body towards food or from danger, *organs of offence and defence*, such as teeth and claws, for procuring food and resisting attack, *organs of digestion*, such as the stomach and bowels, *organs of circulation*, such as the heart and blood vessels, to convey the digested food about the body and to carry waste matters to the *excretory organs*, such as the kidneys, *organs of respiration*, such as lungs and gills, *organs of reproduction*, and so forth. An organ may consist of subsidiary organs. Thus the leg is supported by *skeletal organs* known as bones, moved by *muscles*, and served by blood vessels and nerves. A complex of parts which work together is known as an *organism*, and this name is often applied to animals and to plants, for plants are also provided with organs, and also alive. The provision of separate organs for particular functions is called *organisation* or *differentiation*, the assignment of particular functions to separate organs which corresponds to organisation is called, by analogy with the similar separation of functions in modern industry, *the physiological division of labour*. Organisation exists to a very various extent among organisms, and of two organisms that which has the larger number of different organs is said to be the *more highly organised* or *more highly differentiated*, or simply the *higher*. Thus man is a higher organism than a jelly-fish. There are also great differences in form between the organs of animals of different grades of organisation. Thus an insect is as highly organised as a fish, but its organs are utterly different in form. The differences in structure between animals correspond to differences in the circumstances in

which they live. An animal which lives in water has, for instance, very different organs of locomotion and respiration from one which lives on land, and the sense organs of an internal parasite are much less highly differentiated than those of an animal which has to seek food and avoid enemies from hour to hour. This correspondence between organisation and circumstances is known as *adaptation*.

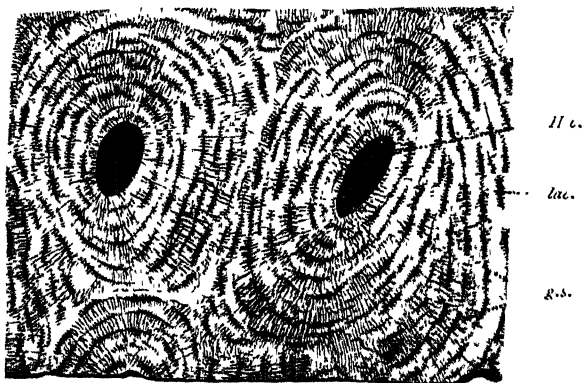


FIG. 4.—A section of dry bone magnified. The dark spaces show where the living part of the tissue was lodged.

lac., Spaces known as "lacunæ." In these lay the cells into which the protoplasm was divided. *g.s.*, ground-substance. This is traversed by numerous "canaliculi" in which processes of protoplasm united the cells into a meshwork. *H.c.*, "Haversian canals," in which minute blood vessels lay. The lacunæ are so arranged as to divide the ground-substance into concentric layers or "lamellæ" around the Haversian canals.

Organisation involves more than the mere existence of organs, more, that is, than the shaping of the body into regions where special functions are performed. It involves also a specialisation of each of these regions to fit it for its special functions. This specialisation is found partly in the shape of each organ, but also largely in its texture and composition. The substance of the body is not alike throughout, but different portions of it have differences in texture and chemical composition which confer upon them different properties,

Tissues.

Thus the outer layer of the skin is firm and hard to penetrate, bone is rigid, blood is fluid, the substance known as "connective tissue" is tough and binds other tissues together,¹ nerve has the power of conduction highly developed, and muscle that of contraction, and so forth. Such a portion of the body-substance with particular properties, due to a particular texture and composition, is known as a *tissue*. An organ may consist of one tissue throughout, but is usually built up of several, upon the nature and arrangement of which its powers depend. Thus a muscle contains, besides muscular tissue, connective tissue to bind it together and nervous tissue to conduct through it the impulses which cause it to contract.

We have hitherto spoken of the body as though it were alive throughout. This, however, is rarely the case. The living part of the body of all animals is a soft slimy substance known as *protoplasm*. In a few cases this forms the whole body, but in most it is only a part. All tissues contain protoplasm, but many contain also a framework of other substances, made and secreted by the protoplasm and serving for its support. Thus in bone (Fig. 4) there is a groundwork, consisting largely of salts of lime, to which it owes its hardness, and this groundwork is penetrated by a meshwork of protoplasm. In composition, protoplasm is a solution in water of organic substances and salts, especially characterised by the presence of proteins. In many cases, as we shall see in a later chapter, the protoplasm is divided into minute units known as *cells* (Fig. 5).

The study of living organisms is known as *Biology*, and is divided into *Botany*, which deals with plants, and *Zoology*, which deals with animals. Now an organism may be regarded from two points of view according as attention is concentrated upon its structure or its functions, though of course the connection of structure with function makes it impossible to study either without reference to the other. The sciences of Zoology and Botany are correspondingly divided each

¹ This may be seen in skinning any large animal. The tough, white material which holds down the skin and binds the muscles together is connective tissue.

into two subordinate sciences, *Anatomy or Morphology*, which deals with the structure of the bodies of animals, and *Physiology*, which deals with their functions. In the following pages we shall regard Zoology in the first place from the anatomical point of view, but shall seek from Physiology light upon the meaning of the structures described, endeavouring to trace in the bodies of the animals studied the

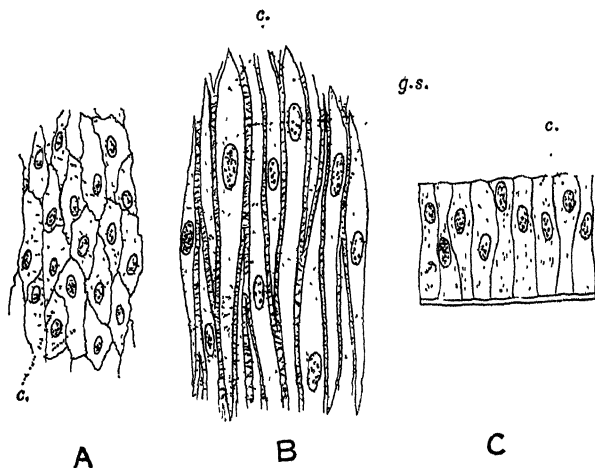


FIG. 5.—Portions of tissues, highly magnified, to show cells.

A, The lining of an artery; *B*, muscular tissue from the wall of the intestine; *C*, the lining of the intestine. *A* and *B* are shown in surface view, *C* in section.

c., Cells; *g.s.*, ground or intercellular substance, traversed by threads of protoplasm from cell to cell.

provision which exists for carrying out all those functions which our first survey has revealed to us as taking place. With this purpose we shall examine in considerable detail first one of the higher animals and then an exceedingly simple example, tracing afterwards, in a series of further examples, the gradual increase in organisation and the varieties that it presents. Finally we shall take opportunity to discuss more fully various aspects and processes of life in the light of further knowledge.

CHAPTER II

THE FROG EXTERNAL FEATURES AND BODY WALL

THE Common Frog of Britain is the species known in Zoology as *Rana temporaria*. It is abundant in summer in damp places, but in winter is less easily found, owing to the fact that it is then in a torpid

Habits

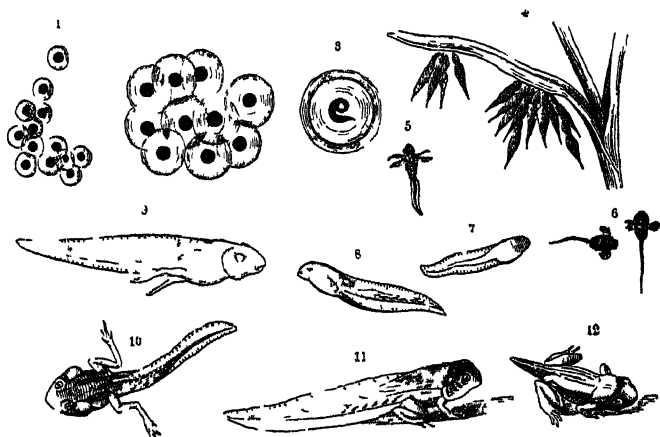


FIG. 6 —The life history of a frog —After Brehm

1-3, Developing ova 4, newly hatched forms hanging to water weeds
5, 6, stages with external gills 7-10 tadpoles during emergence of
limbs 11 tadpoles with both pairs of limbs apparent 12 metamor-
phosis to frog

state hidden in holes or buried in mud. In the spring the warmth wakes the frogs and they congregate, croaking loudly, and pass in the water, where the eggs are laid as a

mass of spawn and fertilised by the sperm which the male sheds over them as they pass out of the female. In about a fortnight there hatches from each egg a little fish-like *tadpole*. This has no limbs, but a strong tail, which it uses for swimming, breathes wholly by gills, and is at first without a mouth. In a few days a mouth appears and the animal begins to feed on vegetable matter. Gradually it changes, losing its gills and tail and gaining lungs and two

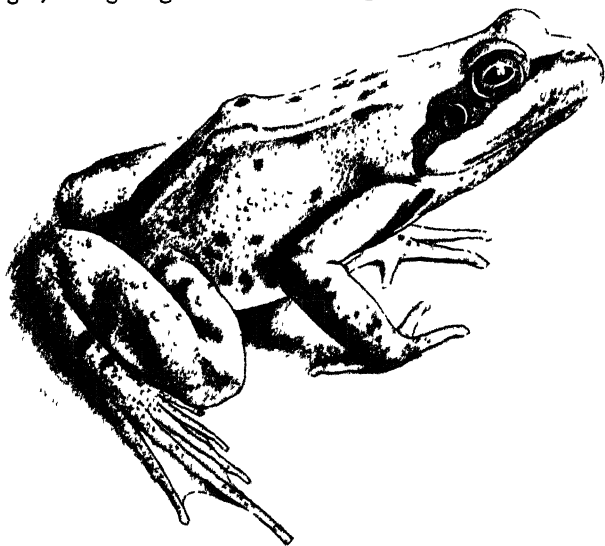


FIG. 7.—The Common Frog.

pairs of limbs, till at the end of three months it becomes a small frog. Henceforward it lives principally on land, sometimes crawling about by means of both pairs of limbs, but generally jumping with the strong hinder pair and using the small fore pair to break its fall when it alights. When it is frightened, however, it occasionally takes to the water, and then swims strongly with its hind limbs. Its food, after it has left the water, consists of slugs, snails, insects, worms, and other small animals, the smaller prey being caught by a sticky tongue, the larger seized with the mouth.

In examining the body of a frog, we are struck, first by the fact that its mottled green and yellow skin is soft and slimy and without the covering of hairs, or scales, or feathers which we find in other animals, and next by its consisting only of head, trunk, and two pairs of limbs. There is no neck or tail. The *trunk* is flattened and bears the head at one end and the limbs of each pair opposite to one another on the narrow sides. In consequence of this symmetrical arrangement we may distinguish a *back or dorsal surface*, a *lower or ventral surface*, right and left sides, and fore and hind ends. Such a symmetry is called *bilateral*, and we shall see that in the frog it extends to the arrangement of nearly all the organs of the body. The *fore or anterior end* is that which is foremost when the animal moves, and is thus the first part to come into relation with objects in the world around it. At this end is placed the *head*, a distinct region of the body, smaller than the trunk, which bears the mouth with which food is taken and the three pairs of principal sense organs by which the animal becomes aware of the nature of its surroundings. The *eyes* are large, and have stout, almost immovable upper lids and thin translucent movable lower lids.¹ The *nostrils or external nares* are a pair of small openings on the top of the head in front of the eyes. Each of them leads into a chamber which communicates with the mouth. There is no flap to the *ear*, but the drum shows upon the surface at the side of the head behind and somewhat below the eye. If the drum be pierced, a bristle passed through it will be found to reach the mouth. On the lower side of the trunk there may be distinguished two regions—the large, soft-walled *belly or abdomen* behind, and the smaller stout-walled *breast region* in front.

The *limbs* of each pair resemble one another, and those of the two pairs correspond roughly in shape, each consisting of three successive parts, the first two slender and the third broad and adapted to be applied to the ground. In the *fore limb or arm* the segment nearest the body is

¹ These do not represent the lower lids of man, which are wanting in the frog. The lower lid of the frog is the *third eyelid or nictitating membrane* found in many other animals. All three eyelids are well developed in birds.

known as the *upper arm or brachium*, the middle segment as the *forearm or antebrachium*, and the third segment as the *hand or manus*. In the hand may be distinguished a *wrist or carpus*, a *palm or metacarpus*, and *fingers or digits*, of which there are only four, that which corresponds to the thumb or pollex of man being absent. The first finger of the male frog bears at the breeding season a rough-skinned swelling, not unlike the ball of the human thumb. In the *hinder limb or leg*, which is longer than the arm, the first segment is known as the *thigh or femur*, the second as the *shank or crus*, the third as the *foot or pes*. The foot contains regions corresponding to those of the

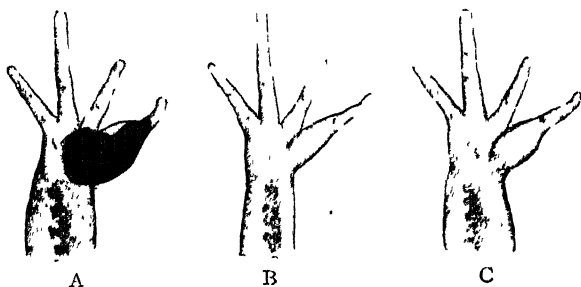


FIG. 8.—The palm of the right hand, *A* of a male frog at the breeding season, *B* of a female, *C* of a male out of the breeding season.

hand, and known respectively as the *ankle or tarsus*, *instep or metatarsus*, and *toes or digits*, but the ankle is much longer than the wrist, and all five toes are present and united by webs of skin, so that a wide surface is provided for use in swimming. The lower side of the foot is called the *plantar surface*, that of the hand the *palmar surface*.

Between the legs at the *hinder or posterior end* of the trunk is the *cloacal opening*, through which are passed the fæces, urine, and eggs or sperm.

The skin of the frog is a thin, tough, protective covering.

Skin.

It contains glands of several kinds, and pigment cells (Fig. 51). Between them the glands provide a slimy liquid, which possesses to a slight extent the acrid property found in the secretion of the skin

of toads and newts. The pigment in the cells expands and contracts in varying conditions of light and temperature and thus alters the colour of the frog. Cold, dark, or wet surroundings cause expansion of the pigment and darkening of the skin. Warmth, light, or dryness cause contraction. From time to time the horny outer layer of the skin is shed and eaten by the frog.

Immediately below the skin is a series of large spaces, the *subcutaneous lymph sacs*, containing a fluid known as the *lymph*. Between the lymph sacs the skin is bound down to the underlying flesh by tough, white connective tissue, but in consequence of the presence of the sacs it is much looser than that of most animals. Below the sacs the body is covered by a continuous layer of flesh, which consists, as the substance so-called always does, of muscles. There is thus a *muscular body-wall*, and this encloses in the trunk a

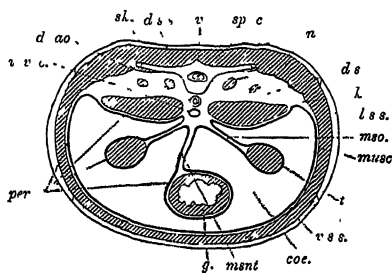


FIG. 9.—A diagram of a transverse section through the abdomen of a male frog.

coe., Coelom; d.ao, dorsal aorta, d.s., dorsal lymph sac; d.s.s., dorsal subcutaneous lymph sac, g., gut, i.v.c., inferior vena cava, k., kidney, l.s.s., lateral subcutaneous lymph sac, meso., mesentery, musc., mesorchium; musc., muscular body-wall, n., spinal nerves; per., peritoneum, sk., skin, sp.c., spinal cord; t., testis, v., vertebra, v.s.s., ventral subcutaneous lymph sac.

large space, the *body cavity or coelom*, in which lie most of the principal *viscera*. The latter name is applied to the soft internal organs of the body, such as the stomach, bowels, liver, lungs, and heart. The body-wall of the back is much thicker than that of the belly, and in it is embedded a structure known as the *backbone, spine, or vertebral column*. This consists of a row of ring-like bones, the *vertebrae*, placed end to end to form a tube, the *vertebral canal*, in which lies a part of the nervous system known as the *spinal marrow or cord*. The muscles of the ventral side are thicker at the ends of the

trunk, where they contain bony hoops, the *shoulder girdle* and *hip girdle*, which, with the vertebræ between the upper ends of each of them, encircle the body. The coelom is lined by a smooth membrane, the *peritoneum*, which is continued over the viscera, so that these are not truly exposed in the body cavity, but hang into it in folds of the peritoneum (Fig. 9). Each fold fits closely over the organ which it suspends, and above the organ the two sides of the fold come together to form a sheet which slings the organ from the body-wall. The largest of these suspensory sheets is that which holds the gut and is known as the *mesentery*. Between the peritoneum and the muscles of the back is on each side a large *dorsal lymph sac*, and in each dorsal lymph sac lies one of the pair of kidneys. In the head there is no body cavity, and the backbone is here continued by a large box of bone and cartilage known as the *skull*, while the spinal cord is prolonged into the skull by the *brain*. The limbs have neither body cavity nor viscera, and among their muscles lie the bones which support them.

The skeleton of the frog is composed chiefly of *bone*, but contains also a good deal of a gristly substance known as *cartilage*. There may be recognised in it an *axial part*, consisting of the skull, backbone, and breastbone, which supports the trunk and head, and an *appendicular part*, comprising the bones of the limbs and their girdles, which supports the arms and legs and anchors them to the trunk.

In the backbone there are nine vertebræ and a long bone, known as the *urostyle*, which represents several vertebræ fused together. The ninth is known as the *sacral vertebra*, and to it is attached the girdle of the hind limbs. Each vertebra consists of a *body or centrum* and an arch, the *neural arch*, placed above the centrum so as to form a ring around the spinal cord. The hollow of each ring is a *vertebral foramen*, and the rings together form the vertebral canal. The roof of each arch is raised into a low ridge, the *neural spine or spinous process*, and in every vertebra except the first the arch bears on each side, just above its junction with the centrum, a *transverse process*, which is especially large in the sacral vertebra. At the end of each transverse process is a

Skeleton :
General
Arrangement.

Backbone.

small knob of cartilage which represents a *rib*. Each vertebra is jointed to those in front and behind it by projections, one on each side at each end of the arch, known as *zygapophyses*. The *zygapophyses* in front of the vertebra (or *prezygapophyses*) have each a flat surface facing upwards. Those behind (the *postzygapophyses*) have flat surfaces facing downwards which fit on to the surfaces of the *prezygapophyses* and slide over them as the backbone bends. Most of the centra are hollow in front and rounded

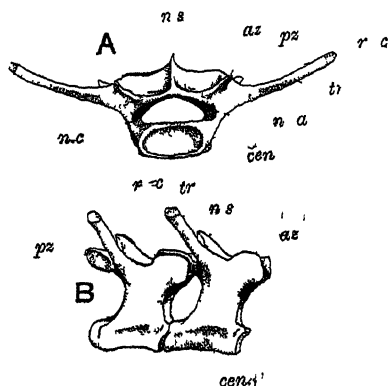


FIG 11.—Vertebra of a frog. *A*, fourth vertebra, seen from in front, *B*, sixth and seventh vertebrae from the right.

az, Prezygapophysis, *cen*, centrum, *na*, neural arch, *nc*, vertebral foramen, *ns*, neural spine, *pz*, postzygapophysis, *rc*, cartilage at end of transverse process, *tr*, transverse process.

behind and thus fit together by ball and socket joints, but the first vertebra has in front two hollows, which serve as sockets for two knobs, known as the occipital condyles, on the hinder end of the skull, while the eighth is hollow behind as well as in front, and the ninth projects in front, to articulate with the hollow of the eighth, and has behind two knobs which articulate with two hollows on the urostyle. The latter is a long, taper-

ing bone with a ridge above, in the front part of which is a canal for the hinder part of the spinal cord.

In the skull, the following regions may be distinguished

Skull (1) the *cranium* or *brain case*, (2) the *nasal capsules*, which enclose the organs of smell, (3) the *auditory capsules*, which enclose the inner part of the ear, (4) the *visceral arches*, an apparatus which lies below the cranium and is highly developed in a fish and in the tadpole, but in the adult frog is represented only by the jaws and by a structure in the floor of the mouth known as the *hyoid*.

The cranium is an oblong box, from which the nasal capsules project in front and the auditory capsules at the sides of the hinder end, while the bones of the upper jaw form a scaffolding fixed to the capsules and supporting the sides of the head. Between this scaffolding and the cranium is on each side a large space known as the *orbit* in which lies the eye. The hinder part of the cranium, between the auditory capsules, is known as the *occipital region*, the middle part, between the orbits, is known as the *sphenoidal region*, and the front part, immediately behind the nasal capsules, is known as the *ethmoidal region*.

The skull consists of a foundation of cartilage taken over from the tadpole, with certain bones which are formed while the tadpole is changing into

a frog. These bones may be divided into two sets according to the way in which they are formed. Those which arise by the conversion into bone of parts of the original cartilaginous skull are known as *cartilage bones*. Those which appear in development without being thus preformed in cartilage are known as *membrane bones* on account of the membrane, consisting of a sort of connective tissue, which at first occupies the places in which they will appear. The cartilage bones are embedded in the cartilage of the skull

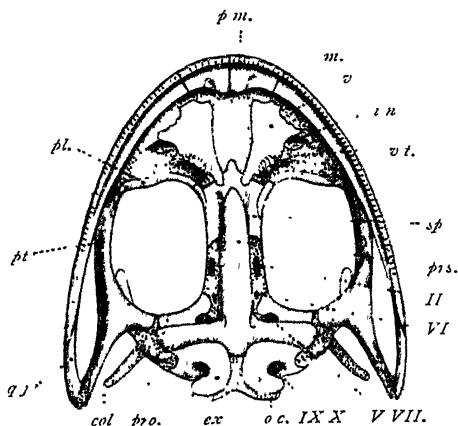


FIG. 12.—The skull of a frog, seen from below.

col., Columella, *ex.*, exoccipital; *i.n.*, internal nares opening, *m.*, maxilla; *o.c.*, occipital condyle, *pl.*, palatine; *p.m.*, premaxilla; *p.r.o.*, prootic, *p.r.s.*, parasphenoid; *pl.*, pterygoid; *q.j.*, quadratojugal; *sp.*, sphenethmoid; *v.*, vomer; *v.t.*, vomerine teeth, *II*, *VI*, *VII*, *IX*, *X*, foramina for cranial nerves.

and cannot be removed, but the membrane bones can easily be taken off.

At the hind end of the cranium is a large opening known as the *foramen magnum* through which the spinal cord is continuous with the brain. On each side of this is a cartilage bone called the *exoccipital* which bears one of the *occipital condyles* mentioned above, but the foramen magnum is not completely bordered by the exoccipitals,

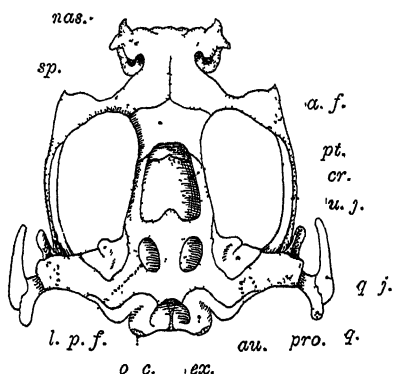


FIG. 13.—The cartilaginous skull of a frog, seen from above after the removal of most of the bones.

a f., Anterior fontanelle, *au*, auditory capsule, *cr.*, cranium, *ex.*, exoccipital; *l p. f.*, left posterior fontanelle, *nas*, nasal capsule; *o c*, occipital condyle, *pro.*, prootic, *pt.*, pterygoid, *q*, quadrate; *q j.*, quadratojugal, *sp*, sphenethmoid; *u. j.*, upper jaw bar

since these are separated above and below by cartilage. The rest of the cranium is mainly composed of cartilage covered by certain membrane bones, but the front end is formed by a cartilage bone known as the *sphenethmoid*. This has the form of a dice box divided across the narrowest part by a transverse partition which closes the cranial cavity in front. A longitudinal partition divides the front half of the box into two. The roof of the cartila-

ginous cranium is pierced by three large holes or *fontanelles*, but these are not seen in an intact skull, since the whole roof is covered, from the exoccipitals to the sphenethmoid, by two long bones, the *frontoparietals*, placed side by side. The floor is complete, and under it lies a large dagger-shaped bone, the *parasphenoid*, placed with the blade of the dagger forward and the crosspiece of its hilt under the auditory capsules.

The wall of the cranium is pierced by certain openings or *foramina*, for the passage of the nerves which arise from

the brain These "cranial" nerves are ten in number on each side The *first nerve* of each side passes through a foramen in the transverse partition of the sphenethmoid on its way from the organ of smell in the nasal capsule The *second nerve*, which serves the eye, enters the skull through a conspicuous opening on each side in the middle of the sphenoidal region The *third and fourth nerves* have each a minute foramen in the side of the same region The *fifth and seventh nerves* pass through a large common opening on the under side of the skull, situated in a notch in the prootic bone mentioned below The foramen for the *sixth nerve* is a small opening between those for the second and for the fifth and seventh The *eighth nerve* enters from the inner part of the ear by an opening in the wall between the cranium and the auditory capsule A foramen for the *ninth and tenth nerves* is situated in the exoccipital bone, at the side of the occipital condyle

The nasal capsules are a pair of irregular, mainly cartilaginous enclosures continuous with the front end of the cranium Only their hinder part is ossified, and this forms that part of the sphenethmoid which lies in front of its transverse partition The wall between the two capsules is known as the *mesethmoid* Through these capsules pass the passages from the nostrils to the mouth, and each of them has therefore an opening above and below Each bears two membrane bones, one on its upper side and one beneath The upper bone is known as the *nasal* and is shaped like the outline of a pear, with the stalk directed outwards The lower bone is the *vomer* It is of irregular shape and carries a patch of teeth which project through the skin of the roof of the mouth

The auditory capsules are blocks of cartilage continuous with that of the cranium Each contains a complicated space, the *cartilaginous labyrinth*, which lodges a structure known as "the membranous labyrinth of the ear" Part of the front of the capsule is ossified to form the *prootic bone* Above these there abuts on its outer side a T shaped membrane bone known as the *squamosal*, which touches it by one limb of the crosspiece of the T, the main limb being directed outwards and downwards At one spot on the outer side of the capsule the cartilage fails and the

labyrinth is covered only by membrane. This gap is known as the *fenestra ovalis*, and from it a slender rod of bone and cartilage, the *columella auris*, runs to the drum of the ear, so that when the latter is thrown into vibrations by sound waves its movements are transferred by the columella to the labyrinth through the membrane.

The framework of the upper jaw is composed of two series of structures, an outer, which borders the opening of the mouth, and an inner, which supports the outer. The inner series is known as the *palato-pterygo-quadrate* on account of the parts of which it is composed. These are as follows. From the junction of the cranium with

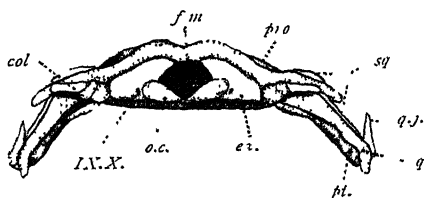


FIG. 14.—The skull of a frog, seen from behind.

col., Columella; *ex.*, exoccipital, *fm.*, foramen magnum, *o.c.*, occipital condyle; *pio*, prootic; *pt.*, pterygoid; *q.*, quadrate, *q.j.*, quadratojugal, *sq.*, squamosal, *I.X.X.*, foramen for ninth and tenth cranial nerves

the nasal capsules there projects outwards a bar of cartilage, against the hinder, or orbital, side of which lies a membrane bone known as the *palatine*.¹ At its outer end the cartilaginous bar turns backwards, and here another membrane bone, the *pterygoid*,¹ fits

against its inner side. The pterygoid is Y-shaped, with the fork directed backwards, the inner branch of the Y abutting on the auditory capsule. The outer branch underlies the main branch of the squamosal, and between these two bony bars there projects outwards from the auditory capsule a rod of cartilage known as the *quadrate*. With the end of the quadrate, held firm as it is above and below by processes of the squamosal and pterygoid, articulates the lower jaw, for which the structures in question are said to form the *suspensorium*. The outer series of bones of the upper jaw begins with the *premaxilla*, a small membrane bone applied

¹ The palatine and pterygoid are cartilage bones in most of the animals in which they occur. In the frog the cartilage bone is replaced in development by membrane bone.

to the front of the nasal capsule, on to whose upper surface it sends a process. The two premaxillæ meet in the middle line, forming the tip of the upper jaw, and each of them bears a row of teeth. Behind the premaxilla, on each side, another membrane bone, the *maxilla*, continues the edge of the jaw. The maxilla is a long slender bone which bears a row of teeth. Along the greater part of its length it is supported by the nasal capsule and pterygoid, but the hinder part lies free till it meets a small cartilage bone, the *quad ratojugal*, which connects it with the quadrate.

The lower jaw or *mandible* consists of two halves united in front by a ligament. Each half is a curved rod of cartilage, known as *Meckel's cartilage*, ossified at the end to form the small *mentomeckelian* bone, and almost completely en-

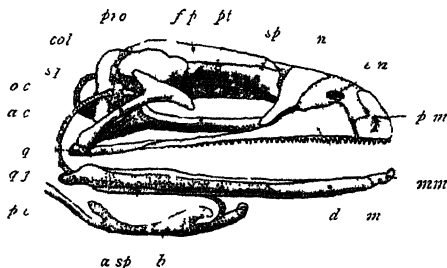


FIG 15 —The skull of a frog, seen from the right side

a c, Anterior cornu of hyoid, *a sp*, angulo splenial *b*, body of hyoid *col*, columella *d*, dentary *en*, external nasal opening *fp*, fronto parietal *m*, maxilla *mm*, mentomeckelian *n*, nasal *oc*, occipital condyle *pc*, posterior cornu of hyoid *pm*, premaxilla, *pro*, prootic *pt*, pterygoid *q*, quadrate, *qj*, quadratojugal *sp*, sphenethmoid *sq*, squamosal

sheathed by a couple of membrane bones, the *angulo-splenial* within, and the *dentary* without. The latter does not, as its name would imply, bear teeth, the frog having no teeth in the lower jaw. At the near end or *angle* of the jaw the dentary bears a small knob or *condyle*, which fits into a hollow, known as the *mandibular fossa*, on the end of the quadrate.

The hyoid is a flat structure in the floor of the mouth. It consists of a wide *body* with two short processes on each side and two longer processes, the *cornua*, at each end. The *anterior cornua* are very long and slender and curve backwards at the sides of the body and then upwards to

be attached to the sides of the auditory capsules. The *posterior cornua* are shorter and stouter and project backwards at the sides of the windpipe. They are the only ossified parts of the hyoid, the remainder consisting of cartilage.

The following table represents in a summary form the architecture of the skull.

<i>Regions of skull.</i>	<i>Cartilage bones.</i>	<i>Membrane bones.</i>
Cranium	{ Exoccipitals Sphenethmoid (part)	Fronto-parietals. Parasphenoid.
Nasal Capsules	{ Sphenethmoid (part) Mesethmoid	Nasals. Vomers.
Auditory Capsules	Prootics	Squamosals ¹
Visceral Arches—		
Upper jaw	{ (Palatines ²) (Pterygoids ²)	Premaxillæ. Maxillæ. Quadratojugals.
Lower jaw	Mentomeckelians	{ Angulo-splenials. Dentaries.
Hyoid	Posterior cornua	None.

The *shoulder girdle or pectoral arch* is a flat structure of cartilage and bone embedded in the body-wall of the forepart of the trunk, which it almost encircles. It consists of two similar halves, one on each side of the body, united below but separate above, where they are bound by muscles to the backbone. Each half is composed of an upper *scapular portion or shoulder blade* and a lower *coracoid portion*. The uppermost part is a broad, flat plate lying on the back known as the *supra-scapula*. A great part of this consists of cartilage stiffened by calcareous matter, but it has a narrow rim of plain cartilage and a core of true bone ³ lies at its outer end, where it joins the *scapula*, a narrower but stouter bone lying at the side of the body. A forward projection from this

¹ Attached to auditory capsules but not belonging to them.

² Cartilage bones in many animals. In the frog only the first rudiment is cartilage bone and this is replaced in development by membrane bone.

³ The structure of bone has already been alluded to. It will be more fully described together with that of cartilage in a later chapter. Bone differs from cartilage not in the mere presence of calcareous matter, but in structure and composition.

bone is known as the *acromion process*. To the lower end of the scapula is attached the coracoid portion of the girdle. This is a plate of cartilage and bone lying on the under side of the body in the breast region and pierced by a wide oval space called the *coracoid fontanelle*. Behind the fontanelle lies the stout *coracoid bone*, in front is a narrow strip of calcified cartilage, the *precoracoid*, continuous with another strip known as the *epicoracoid* which forms the inner border of its half of the girdle and lies against its fellow in the middle line. This junction of the two halves of the girdle is known as its *symphysis*. The only membrane bones in

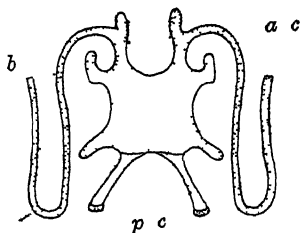


FIG 16 —The hyoid apparatus of a frog

a c, Anterior cornua *b* body
p c, posterior cornua

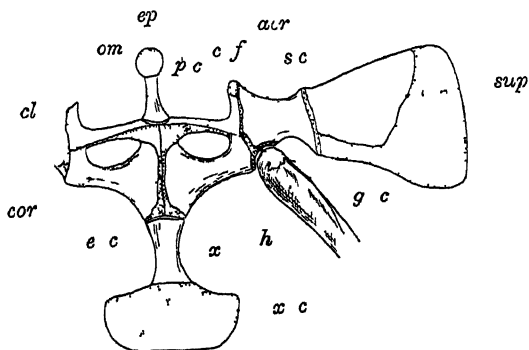


FIG 17 —The shoulder girdle of a frog, seen from below, with the right scapula removed

acr, Acromion process *cf*, coracoid fontanelle *cl*, clavicle *cor*, coracoid, *ec* epicoracoid, *ep*, episternum *gc* glenoid cavity *h*, head of humerus, *om*, omosternum, *pc*, precoracoid *sc*, scapula, *sup*, suprascapula, *x*, xiphisternum, *xc*, xiphoid cartilage

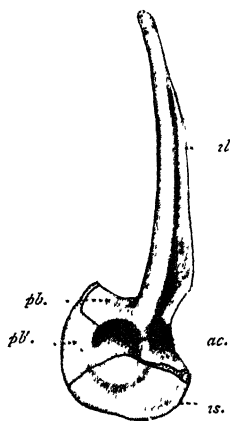
the girdle are the *clavicles*. They are a pair of slender structures which overlie the precoracoid cartilages. Each

sends forward a prolongation beside the acromion process. At the junction of the scapula and coracoid bones is the *glenoid cavity*, a hollow lined by cartilage on the hinder edge of the girdle, into which fits the head of the humerus or bone of the upper arm.

To the ends of the epicoracoids, before and behind the girdle, are attached certain structures which are analogous to the *breastbone or sternum* of other animals. In front is a

bone known as the *omosternum*, bearing at its end a small plate of cartilage, the *episternum*. Behind is the larger *xiphisternum*, bearing the broad, flat *xiphoid cartilage*.

The *hip girdle or pelvic arch* lies at the hinder end of the trunk in a position similar to that occupied in front by the shoulder girdle, which it also resembles in consisting of two halves, each composed of several pieces, joined below in a symphysis. Its shape, however, is very different; it is connected with the backbone not solely by muscles, but also by joints or articulations with the large transverse processes of the sacral vertebra; it bears no bone comparable with the clavicle, and there are in connection with it no



ac, Acetabulum; *il*, ilium, *is*, ischium; *pb*, pubic region of ilium, *pb'*, post-pubic cartilage.

unpaired structures such as the sternum. The greater part of each half consists of a long slender bone, the *hip-bone or ilium*, corresponding in position to the scapular part of the shoulder girdle, which runs downwards and backwards from the sacral vertebra, curving inwards on the under side of the body to join its fellow. The junction is enlarged into a flattened mass by the addition of several elements which are more distinct while they are being formed in development than they are in the adult. Behind lies a ridge of bone known as the *ischium*, which consists at first of two parts, one belonging to each half of the girdle. A

slight groove marks the limits of this bone. In front a similar ridge, not marked off from the ilium, is known as the *pubis*, and represents a pair of pubic bones found in certain other animals, though its relation to the bones so called in man is uncertain. Ventrally, between the pubis and the ischium, lies a triangular piece of calcified cartilage, the *postpubic cartilage*. In each of the flat sides of the mass formed by the union of these structures is a round hollow, the *leg-socket or acetabulum*, into which fits the head of the thigh-bone.

The upper arm contains a single bone, the *upper arm bone or humerus*. This consists of a stout shaft, swollen at each end, and bearing on its inner side a ridge known as the *deltoid ridge*. The swelling at the upper end is the *head*, and fits into the glenoid cavity of the shoulder girdle. That at the lower end, the *trochlea*, is more irregular in shape and serves for the articulation of the *forearm bone or radio-ulna*. In man, and in most animals whose limbs are built upon the same plan as those of the frog, the forearm contains two bones, the *radius* and the *ulna*, and traces of the fusion of these can clearly be seen in the frog. The radius is the inner of the two components of the bone, but its upper end lies partly in front of the ulna.¹ The upper end of the radio-ulna is hollowed to receive the humerus at the elbow-joint, behind which it projects as the *elbow-bone or olecranon process*. The wrist consists of six small *carpal bones* arranged in two rows across the limb. Those of the first row are named according to their position *radiale*, *intermedium*, and *ulnare*. The second row contains in the early stages of its development five bones, called *distal carpals*, corresponding to five digits, but in the adult frog the third, fourth, and fifth of these have fused.² The palm contains five *metatarsal bones*. The first digit is wanting, but the second and third have each two bones and the fourth and fifth three, according to the number of their joints. These bones are called *phalanges*.

The bones of the leg correspond closely to those of the

¹ See p. 347.

² In many animals a bone known as the *central or centrale* lies between the two rows of bones of the wrist.

arm. The *thigh-bone* or *femur* has a long, slender, slightly curved shaft with a rounded *head* to fit into the acetabulum and a wide *condyle* for articulation with the *shank-bone*, *os cruris*, or *tibio-fibula*. The latter, like the radio-ulna, corresponds to two bones in man and many other animals, showing traces of being formed by the fusion of an inner or anterior *shin-bone* or *tibia* and an outer or posterior *fibula*. The ankle, like the wrist, consists of two rows of bones, which are here called *tarsals*. The first row contains

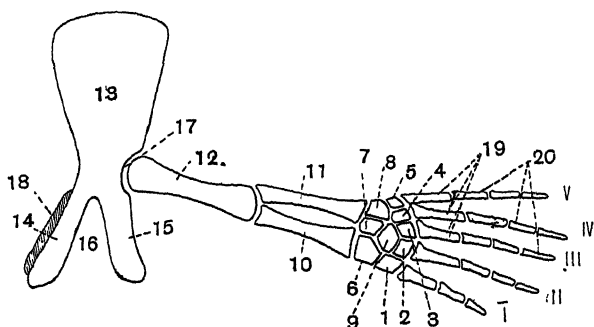


FIG. 19.—A diagram to illustrate the structure of the limbs and girdles of pentadactyl animals.

1-5, Distal carpals or tarsals; 6, radiale or tibiale; 7, intermedium; 8, ulnare or fibulare; 9, centrale; 10, radius or tibia; 11, ulna or fibula; 12, humerus or femur; 13, scapula or ilium; 14, precoracoid or pubis; 15, coracoid or ischium; 16, coracoid fontanelle or obturator foramen; 17, glenoid cavity or acetabulum; 18, clavicle; 19, metacarpals or metatarsals; 20, phalanges; I-V., digits.

two bones, the *tibiale*, *astragalus*, or *talus* and the *heel-bone*, *fibulare*, or *calcaneus*. These bones are joined at each end by a piece of cartilage. The second row consists of two small *distal tarsals*. The metatarsus contains six *metatarsals*, one minute, corresponding to a small extra toe, the *prehallux* or *calcar*, which lies inside the first toe or hallux, but does not project from the foot. The calcar has one phalanx, the first two toes have each two, the third and fifth toes three, and the fourth toe, which is the longest, has four.

It will be seen that the fore- and hind-limbs and girdles are built upon a common plan. This is shown in Fig. 19. It is not peculiar to the frog, but may be traced in all animals which have fingers and toes. Neither of the limbs of the frog conforms to it exactly.

The movements of the body and of its organs are brought about by means of a tissue known as *muscle*.
Muscles. This tissue is classed according to its function as *voluntary* when it is under the direct control of the will and *involuntary* when it is not under such control. Involuntary muscle generally forms part of the wall of some internal organ such as the stomach, bowel, bladder, or heart, and by its contraction brings about changes in the width of this organ and thus movement of the fluid it contains. Voluntary muscle is usually found in the form of distinct organs or *muscles*, which are attached at their ends to two parts of the skeleton and by their contraction change the relative position of these parts and thus of the regions of the body which they support. Sometimes the end of a muscle may be attached by a stout band or *aponeurosis* of connective tissue to another muscle. There is, generally speaking, also a difference in fine structure between voluntary and involuntary muscle, but we shall postpone discussion of this for the present. A muscle has a *belly* of muscular tissue which is attached by *tendons* of a peculiar kind of connective tissue. One of the two attachments is called the *origin*, and this is made to a relatively fixed part; the other, called the *insertion*, is made to a more movable part. Parts of the skeleton which are thus movable upon one another must be provided with *joints*. When the amount of movement which is possible is small, the joint consists of an intervening layer of cartilage or ligament, and is said to be *imperfect*. This kind of joint is found, for instance, between the bones of the frog's shoulder girdle. When free movement is possible there is a *perfect joint*. Here a convex surface of one structure plays within a concave surface of another, the two surfaces being separated by a fibrous bag, the *synovial capsule*, which contains a watery fluid, the *synovia*, and serves as a cushion. Outside the joint, ligaments hold the movable pieces together. The muscular system of the frog

is complicated, and we shall therefore only give an outline of its general arrangement and mention a few of the more important muscles.

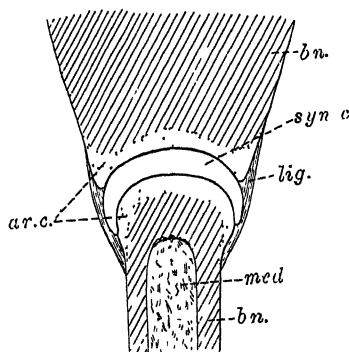


FIG. 20.—A diagram to illustrate the structure of “perfect” joints.

ar.c., Articular cartilage, *bn*, bone, *lig.*, ligament; *med*, medulla or marrow, *syn.c.*, synovial capsule

The following table sets forth the *general arrangement of the muscular system*.

A. MUSCLES OF THE TRUNK.

1. *Muscles of the lower side.*

a. *Muscles of the Belly.*

e.g. *Rectus abdominis*, a wide band running along the belly, divided lengthwise down the middle by the connective tissue *linea alba* and transversely by *tendinous intersections*.

Obliquus externus, a broad sheet at each side of the body, arising from an aponeurosis known as the *dorsal fascia* which covers the muscles of the back, and inserted into the *linea alba* above the *rectus abdominis*.

Obliquus internus and *transversus*, muscular sheets within the external oblique.

By their contraction all these muscles lessen the size of the body cavity and compress the organs within it.

b Muscles of the Breast Region

e.g. *Pectoralis*, large and fan shaped, inserted into the deltoid ridge of the humerus and consisting of a *sternal portion* which arises from the pectoral girdle, and an *abdominal portion* which arises from the aponeurosis at the side of the rectus abdominis. It draws down the arm.

Coraco radialis, arising from the coracoid and inserted into the upper end of the radius. It bends the arm.

2 *Muscles of the Back*

a Muscles inserted into the lower jaw

Depressor mandibulae, triangular, arising from the suprascapula and inserted into the angle of the lower jaw, which it draws downwards and backwards, thus opening the mouth.

b Muscles inserted on the fore limb

e.g. *Latissimus dorsi*, triangular, arising from the dorsal fascia and inserted into the deltoid ridge. It draws back the arm.

Infra spinatus, in front of and similar to the latissimus dorsi. It raises the arm.

c Muscles inserted into the shoulder girdle

e.g. *Levator anguli scapulae*, arising from the skull and inserted into the under side of the suprascapula, which it draws forward.

Serratus, arising from the little knobs on the transverse processes of the vertebrae which represent the ribs, and inserted into the under side of the suprascapula, which it draws backwards, outwards, or inwards according to the division which is contracted.

d Muscles inserted into the hind limb

e.g. *Gluteus*, arising from the ilium and inserted into the femur, which it rotates inwards.

e Muscles inserted into the hip girdle

e.g. *Coccygeus iliacus*, arising from the urostyle and inserted into the ilium, which it holds firm as a fulcrum for the movements of the hind limb.

f Muscles of the Backbone

e.g. *Longissimus dorsi*, a band running the whole length of the back, divided by tendinous inter sections, which are attached to the transverse processes, and inserted in front into the skull. It straightens the back.

B MUSCLES OF THE HEAD

I *Muscles underneath the Head*

e.g. *Sternohyoid* from hyoid to pectoral girdle

Geniohyoid from hyoid to chin

Hyoglossus from hyoid to tongue

Petiohyoid from hyoid to auditory capsule,

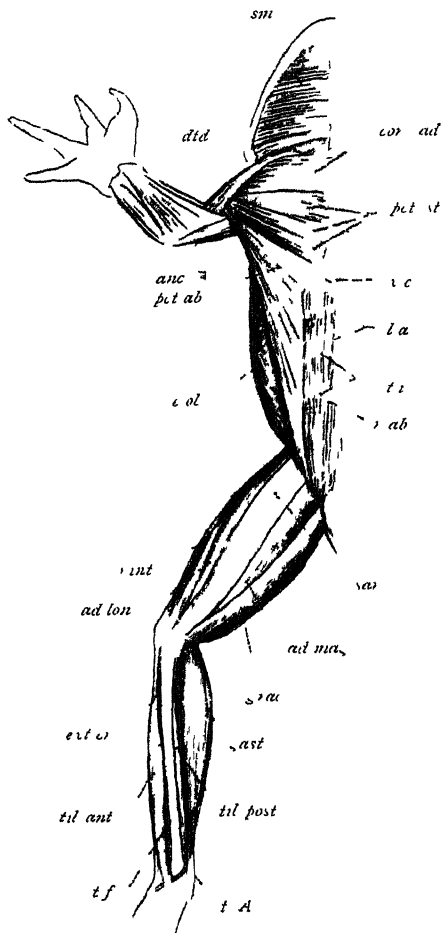


FIG 21 —A ventral view of the muscular system of a frog

ad long, Adductor longus *ad mag*, adductor magnus *anc*, anconaeus *cor rad*, coraco radialis *dtd*, deltoid *ec*, extensor carpi *gast*, gastrocnemius *grac*, gracilis *la*, linea alba *pet ab*, abdominal part of the pectoral muscle *pet st*, sternal part of the same *r ab*, rectus abdominis, *sar*, sartorius *sm*, mylohyoid *ti*, tendinous intersections, *tA*, tendo Achillis *tf*, tibiofibula *tib ant*, tibia anterior, *tib post*, tibia posterior, *v int*, vastus internus *ec*, apophysis cuticularis

Mylohyoid, submandibular, or submaxillaris, a sheet of muscle running from side to side of the lower jaw

These muscles alter the position of the floor of the mouth

2 *Muscles of the Lower Jaw*

e.g. *Temporalis and masseter*, arising from the skull and inserted into the lower jaw, which they raise

3 *Muscles of the Eyeball*

Rectus superior, r inferior, r externus, r internus, arising from the skull in the hinder part of the orbit and inserted into the eyeball

Obliquus superior and o inferior, arising from the skull in the front part of the orbit and inserted into the eyeball

These muscles will be more fully described in the chapter on the dogfish

C MUSCLES OF THE FORE LIMB

1 *Muscles for the Upper Arm*

e.g. *Deltoides*, arising from the scapula and inserted into the humerus. It raises the arm

2 *Muscles for the Fore Arm*

Triceps brachii or anconæus, arising from the scapula and humerus, and inserted into the upper end of the ulna. It straightens the arm

There is no *Biceps* muscle in the arm of the frog

3 *The muscles of the wrist and fingers* are numerous and complicated

D MUSCLES OF THE HIND LIMB

1 *Muscles of the Thigh*

e.g. *Adductor magnus*, a large muscle arising from the pubis and ischium, lying on the part of the thigh, and inserted into the femur near its lower end. It draws the thigh towards the body

Sartorius, a long, narrow band arising from the lower end of the ilium, lying obliquely upon the adductor magnus, and inserted into the tibia on its inner side near the end. It bends the knee

Gracilis or rectus internus femoris, a large muscle arising from the ischium, lying along the inner side of the adductor magnus, and inserted into the inner side of the head of the tibia. It bends the knee

Semimembranosus, a stout muscle arising from the ischium, lying on the back of the thigh, and inserted into the back of the head of the tibia. It bends the knee

Triceps extensor cruvis, a very large muscle inserted into the front of the tibia just below the head of the latter, but arising from the pelvic girdle as three separate muscles, the *rectus anterior femoris*, *vastus externus*, and *vastus internus or crureus*. All these lie on the front of the thigh, and their action is to straighten the knee

2. *Muscles of the Shank.*

e.g. *Peroneus*, a long muscle which arises from the end of the femur, lies along the side of the tibio-fibula, and is inserted into the end of the tibia and the calcaneum. It straightens the leg.

Gastrocnemius, a large, spindle-shaped muscle which forms the "calf." It arises from the hinder side of the end of the femur and tapers into the long *tendo Achillis*, which passes under the ankle joint and ends in the sole of the foot. It straightens the foot on the shank.

Tibialis anterior, arising from the front of the femur by a long tendon, lying in front of the shank, and dividing into two bellies, which are respectively inserted into the astragalus and calcaneus. It bends the foot on the shank.

3. The *muscles of the ankle and toes* are numerous and complicated.

CHAPTER III

THE FROG. VISCERA AND VASCULAR SYSTEM

THE food of the frog is received and digested by a winding tube, known as the *gut or alimentary canal*, which runs from mouth to cloacal opening and is lined by a soft, glandular *mucous membrane*. The *gape* of the mouth lies between two *jaws*,

Alimentary System.

of which the upper is not movable, but the lower is hinged. There are no *teeth* in the lower jaw, but the upper bears a row of maxillary teeth, and a patch of vomerine teeth is found on each side of the roof of the mouth. The teeth are small, sharp-pointed structures, consisting of a *base* and a spike or *crown*. The greater part of the crown is composed of *ivory or dentine*, but the base is formed of bone, and the crown is covered by a cap of very hard substance known as *enamel*, and both are pierced by a core of soft tissue called the *pulp* (Fig. 23). The teeth are all alike, and all fused to the surface of the bones that carry them. As they are destroyed by use

they fall out and are replaced one by one. On the front part of the roof, at the side of the vomerine teeth, open the *internal nares*. The tongue is a muscular structure arising from the front part of the floor of the mouth and forked at its free end, which is directed backwards when it is at rest. In taking food the tongue is turned over and its free end thrown out of the mouth, wiping up, as it goes, a sticky substance secreted by glands in the roof of the mouth,

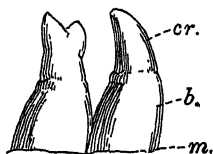


FIG. 22.—Two of the maxillary teeth of a frog, seen from the outside of the jaw.

b., Base of the tooth; *cr.*, crown; *m.*, edge of the maxilla.

so that the prey adhere to it. Behind the angle of the jaw is a region known as the *pharynx*, into which open, at the sides of its roof, the pair of *Eustachian tubes* which lead to the drum of the ear, and below, in the male, a pair of *vocal sacs* which are inflated and act as resonators during croaking.

In the middle of the floor of the pharynx is a slit-like opening, the *glottis*, which leads into the wind-pipe.

From the pharynx a tube known as the *gullet* or *œsophagus* leads backwards in the body cavity to the *mauw* or *stomach*, which is spindle-shaped and separated by a slight constriction, the *pylorus*, from the *bowel* or *intestine*. The first part of the intestine, known as the *duodenum*, is narrow and turns forward so as to lie parallel with the stomach. It is succeeded by another narrow tube, the *ileum*, which runs backwards in several coils. Duodenum and ileum are together known as the *small intestine*: at its hinder end this region opens suddenly into a much wider tube, the *large intestine* or *rectum*. The length of the small intestine is from 4 to 5 inches; that of the large intestine is

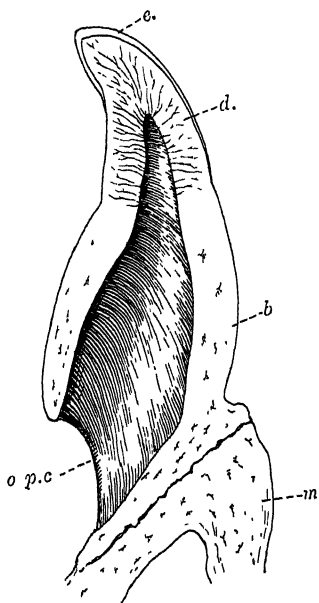


FIG. 23.—A vertical section through a tooth and part of the maxilla of a frog.

b, Base of the tooth, composed of bone (cement); *d*, dentine, *e*, enamel; *m*, maxilla; *o.p.c.*, opening of the pulp cavity.

about an inch and a quarter. The internal surface of the intestine is increased by folds of its lining. These are transverse in the duodenum and longitudinal in the ileum. The rectum passes into a region known as the *cloaca*, which receives ventrally thin-walled, bilobed sac, the *urinary*

bladder, and dorsally the ducts of the kidneys and in the female those which bear the eggs.

Besides numerous small *glands* in the mucous membrane, the alimentary canal receives the secretions of two large glands, the liver and the pancreas. The *liver* is a large, reddish-brown structure in the forepart of the belly. It consists of a right and a left lobe and a small median lobe

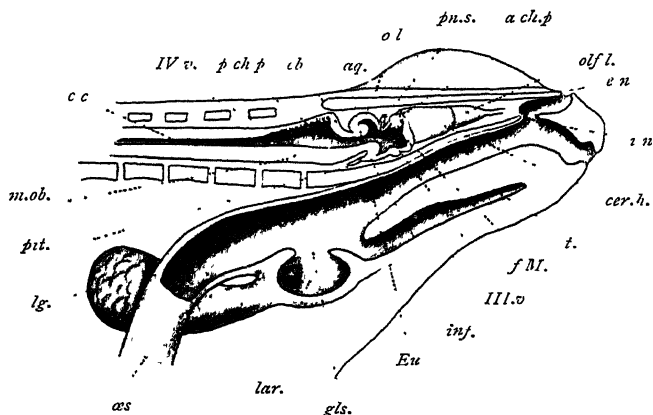


FIG. 24.—A longitudinal median section through the head of a frog.

aq., Aqueduct of Sylvius, *a.ch.p.*, anterior choroid plexus, *c.c.*, central canal of spinal cord, *cb*, cerebellum; *cer.h.*, left cerebral hemisphere, *e.n.*, nostril; *Eu*, Eustachian tube; *f.M.*, foramen of Monro, *gls.*, glottis, *i.n.*, internal nares opening; *inf.*, infundibulum; *lar.*, larynx; *lg.*, left lung; *m.ob.*, medulla oblongata; *ol*, optic lobe; *as*, oesophagus; *olf.l.*, olfactory lobe; *p.ch.p.*, posterior choroid plexus; *pit.*, pituitary body; *pn.s.*, pineal stalk; *III.v.*, third ventricle; *IV.v.*, fourth ventricle.

which unites them. The left lobe is the larger and is itself deeply cleft into two. Between the right and left lobes lies the *gall-bladder*, which receives the green bile secreted by the liver and passes it by the *bile-duct* into the duodenum. The *pancreas* is an oblong, creamy-white structure lying between the stomach and duodenum. It is traversed by the bile-duct, into which it passes the pancreatic juice which it secretes.

The food is not chewed, but is swallowed whole, the only use of the teeth being to prevent the escape of the

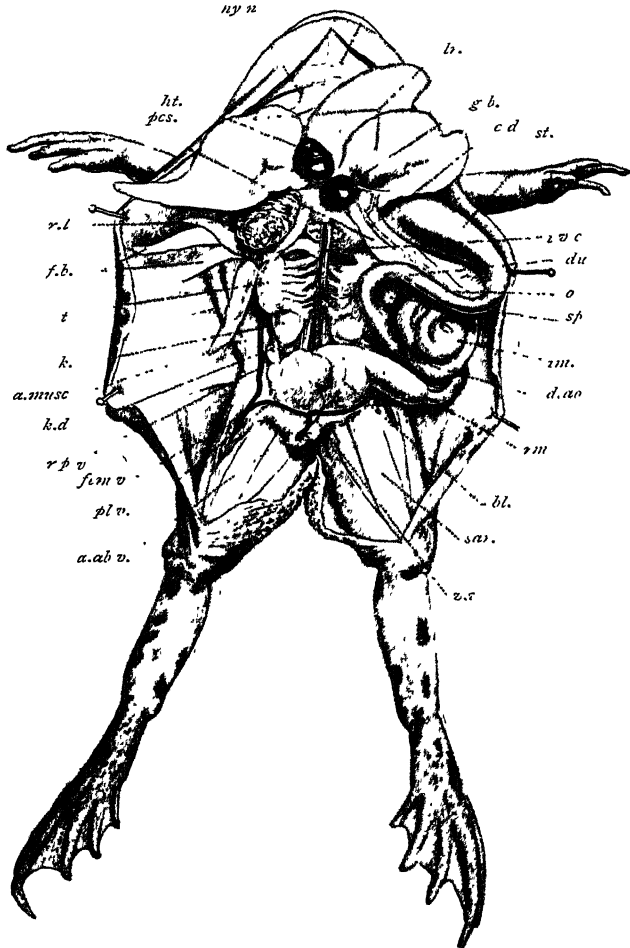


FIG. 25.—A male frog dissected from the ventral side.

a.ab.v., Anterior abdominal vein, cut short, ligatured, and turned back; *a.musc.*, cut edge of abdominal muscles; *bl.*, urinary bladder; *c.d.*, common duct of gall-bladder and pancreas; *d.a.o.*, dorsal aorta; *du.*, duodenum; *f.b.*, fat body, *fem.v.*, femoral vein; *g.b.*, gall-bladder; *ht.*, heart; *hy.n.*, hypoglossal nerve, *im.*, ileum, *i.v.c.*, inferior vena cava, *k.*, kidney; *k.d.*, kidney duct with vesicula seminalis; *l.*, liver; *o.*, point at which *c.d.* enters the duodenum; *pcs.*, pancreas; *pl.v.*, pelvic vein; *r.l.*, right lung; *rm.*, rectum; *r.p.v.*, renal portal vein; *sar.*, sartorius muscle, *sm.*, myolohoid muscle; *sp.*, spleen, *st.*, stomach; *t.*, testis; *v.v.*, vesical vein.

prey, for which reason they are directed backwards. In the stomach the food meets the *gastric juice*, secreted by the glands of the mucous membrane of the stomach. This juice is acid and contains an organic substance known as *pepsin*, which turns proteids into more soluble materials. Here the food is killed, disinfected of harmful bacteria by the acid, and partly dissolved by the action of the pepsin. Pepsin is an example of an exceedingly important class of substances, found in living bodies, which resemble the "catalytic agents" of the chemist in having the power of bringing about changes in other substances without themselves undergoing change, and of doing this even though they be present in very small quantities in a large mass of the substance acted upon. These agents are called *ferments or enzymes*. From time to time a ring of muscle known as the *pyloric sphincter*, which guards the opening of the duodenum, relaxes and lets through partly digested food into the intestine, where it meets three alkaline juices, the *bile*, the *pancreatic juice*, and a juice known as the *succus entericus*, which is secreted by the intestinal wall. Of these the pancreatic juice is the most powerful, dissolving all three classes of organic food-stuffs (proteids, fats, and carbohydrates, see p. 6), each by means of a distinct enzyme. The action of the bile and succus entericus is subsidiary to that of the pancreatic juice, and the bile is also partly an excretion. The food thus rendered diffusible is absorbed by the activity of the intestinal lining. The movement of the food along the alimentary canal is brought about by the contraction of a muscular layer in its wall (see Fig. 45), waves of contraction passing down its length. This process is called *peristalsis*. Finally the undigested portion of the food passes through the rectum and cloaca to the exterior as the fæces.

The secretion of bile is not the only function of the liver.

Functions of the Liver. That organ is the great chemical workshop and storehouse of the body. In it a part of the excess of carbohydrate and fatty food taken during the summer is stored for use during the winter sleep and the breeding season. The fat is stored in droplets, the carbohydrate in the form of *glycogen* or animal starch, which is converted into sugar when it is to be transferred to other

parts of the body. In the liver also the nitrogenous waste is converted into urea ready for excretion by the kidneys, and various other chemical changes take place.

We must here mention certain organs known as the *ductless glands*, which, while they manufacture substances of importance to the body,¹ discharge these products not through a duct but into the blood or lymph by a process known as *internal secretion*. A similar process takes place in other organs—for instance, as we have seen, in the liver.

The *thyroid glands* of the frog are a pair of small, rounded, pinkish bodies lying on the external jugular veins. Their secretion has an important, but not well understood, action in maintaining the normal working of various parts of the body.

The *adrenal bodies* (so-called *suprarenal glands*) are small yellowish masses lying on the ventral surface of the kidneys. They secrete a substance which has important effects on the "tone" of muscular tissue.

The *thymus* is a small body which lies behind and above the angle of the jaw on each side. Its functions are unknown.

The *pituitary body* or *hypophysis* lies in the skull below the brain (see p. 70). Its presence is essential for life, but its mode of action is not understood.

The *spleen* is a small, round, dark red body, lying in the mesentery opposite to the beginning of the rectum. It is engaged in the manufacture of the little cells which float in the blood and are called "blood corpuscles" (see p. 97), and perhaps also in the destruction of some of them. It is also concerned in the preparation of nitrogenous waste matters for excretion. Its removal is not fatal.

The *fat bodies* are two orange-coloured tufts of flattened processes, attached in front of the ovary or testis to the dorsal wall of the body cavity. They consist of fatty tissue (see p. 95) which, like the reserves in the liver, increases during the summer and decreases during the winter sleep, when it is being drawn upon for the nourishment of the body.

The *heart* of the frog is a hollow, conical, muscular structure, which lies with the apex backwards in the body cavity, between the breast-bone and the gullet. It is enclosed in a thin sac, the *pericardium*, whose cavity is a part of the body cavity

**Vascular
System: Heart.**

¹ It is possible that some of these glands are of importance also in destroying poisonous substances formed in the course of metabolism.

separated from the rest during development, the heart having the same relation to it that the alimentary canal has to the general body cavity—that is, being covered by a continuation of the pericardial membrane as the gut is by the peritoneum. Five chambers may be recognised in the heart. Of these the most conspicuous is the *ventricle*, a large, conical structure, with thick, muscular walls, from which arises in front, on the right side of the ventral surface, the much smaller, tubular *truncus arteriosus*. The *right and left auricles or atria* are relatively thin-walled chambers, the right larger than the left, separated by a septum and lying in front of the ventricle, into which each opens. On the dorsal surface of the heart, opening into the right auricle, lies the still thinner walled, triangular *sinus venosus*.

The openings between these chambers are guarded by certain *valves* or folds of the lining of the heart. Two simple lips of the opening between the sinus and right auricle are the *sinu-auricular valves*; these allow blood to flow into the auricle, but

fold over to prevent its reflux. The edge of the auricular septum is cleft and projects into the ventricle as two flaps, the *auriculo-ventricular valves*. Each of these is connected with the walls of the ventricle by fine cords, the *chordæ tendineæ*, so that, while blood can pass from auricles to ventricle, its reflux is prevented by its raising the valves, which are kept from turning back

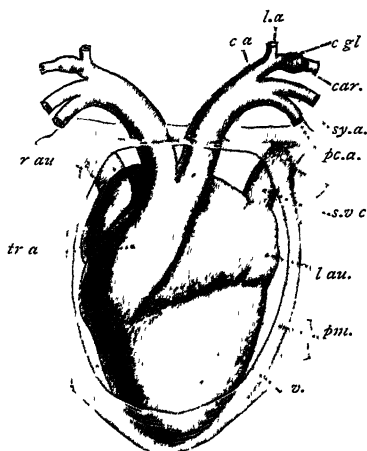


FIG. 26.—The heart of a frog, seen from the ventral side.

c.a., Carotid arch; *car.*, carotid artery; *c.gl.*, carotid gland; *l.a.*, lingual artery; *pc.a.*, pulmocutaneous arch; *pm.*, pericardium; *r.au.*, *l.au.*, right and left auricles; *s.v.c.*, superior vena cava; *sy.a.*, systemic arch; *tr.a.*, truncus arteriosus; *v.*, ventricle.

into the auricle by the chordæ tendineæ. The opening from ventricle to truncus is guarded by three *semilunar valves*, shaped like watch pockets, which are spread out by the blood when it tends to flow backwards from truncus to ventricle. The truncus arteriosus is divided internally by a *second row of semilunar valves* into two unequal parts, a long *conus arteriosus* or *pylangium* next the ventricle, and a short *ventral aorta* or *synangium*. The conus is incompletely

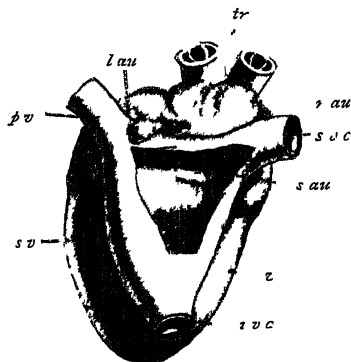


FIG. 27.—The heart of a frog, removed from the pericardium and seen from the back with the sinus venosus opened.

v c, Inferior vena cava, *p v*, pulmonary veins, *rau*, *lau*, right and left auricles, *s au*, opening from sinus to right auricle, *s v c*, superior vena cava, *s v*, sinus venosus, *tr*, branches of truncus cut across, *v*, ventricle.

divided longitudinally by a *spiral valve* into a *cavum aorticum*, which begins on the right side and curves round to become ventral, and a *cavum pulmocutaneum*, which begins on the left side and curves round to become dorsal. The synangium is completely divided into a dorsal and a ventral chamber¹. The dorsal chamber communicates behind with the *cavum pulmocutaneum* and in front with the blood vessel to the lungs (pulmocutaneous arch), the ventral

chamber communicates behind with the *cavum aorticum* and in front with the blood vessels known as the systemic and carotid arches.

The function of the heart is, by the contractions of its muscular wall which are known as its *beat*, to drive blood through the vascular system to all parts of the body. The

¹ The septum which makes this division ends towards the heart by cutting across the hollow of one of the second row of semilunar valves. It is from the outer side of this valve that the spiral valve starts. Thus it comes about that the outer ends of the *cavum aorticum* and *cavum pulmocutaneum* are each guarded by one and a half valves.

contraction starts in the sinus venosus, driving the contained blood into the right auricle. Meanwhile the left auricle is filling by the inflow of blood from the lungs through the pulmonary vein. The auricles now contract simultaneously, driving the blood into the ventricle.

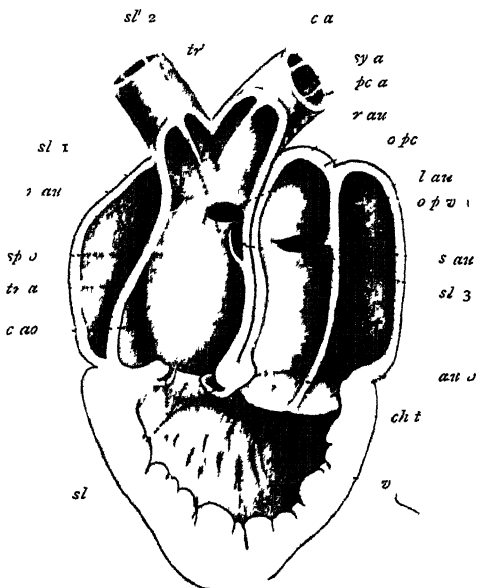


FIG. 28.—A ventral view of the heart of a frog, opened to show the internal structure. The ventral wall of the truncus, ventricle, and auricles has been removed.

au v, Auriculo ventricular valves, *ca*, carotid arch, *cao*, cavum aorticum, *cht*, chordæ tendineæ, *lau*, left auricle, *opv*, opening of pulmonary vein, *opc*, opening of dorsal division of synangium, by which blood passes from the cavum pulmocutaneum to the pulmocutaneous arch, *pc a*, pulmocutaneous arch, *rau*, right auricle, *s au*, sinu auricular opening with valves, *sl*, first row of semilunar valves, *sl'*, semilunar valves of second row, *sl' 1*, the semilunar valve from which the spiral valve starts, the line points to a small portion of the valve which has been cut open, *sl 2*, small semilunar valve at end of cavum pulmocutaneum, *sl 3*, a small part of a large semilunar valve, of which the rest extends across that portion of the front wall of the truncus which has been removed, *sp v*, spiral valve, *sy a*, systemic arch, *tra*, wall of truncus arteriosus, *tr'*, one of the two bundles of arteries into which the truncus divides, *v*, ventricle.

The sinus is beginning to relax, but the reflux of blood into it is prevented by the sinu-auricular valves. The right-hand side of the ventricle receives the blood from the right auricle and the left-hand side that from the left auricle, and these portions of blood mix slowly because a great part of the hollow of the ventricle is spongy, owing to the presence of muscular projections known as *columnæ carneæ*. The ventricle contracts immediately after the auricles, the auriculo-ventricular valves preventing the passage of blood back into the latter. The effect of the contraction of the ventricle is therefore to drive the blood onward into the truncus arteriosus. Since this is on the right side of the ventricle, it will receive first the blood from the right ventricle. Both cavum aorticum and cavum pulmocutaneum are filled, but since the pressure in the carotid and systemic arches is higher than that in the pulmocutaneous arch the blood is driven into the latter. As the ventricle continues to contract the pressure of the blood rises until it is high enough to overcome the resistance in the systemic and finally in the carotid arches. At the same time the contraction of the truncus arteriosus brings the spiral valve into a position in which it shuts off the cavum pulmocutaneum. Thus the blood from the left auricle (and therefore from the lungs), which is the last to enter the truncus, passes along the cavum aorticum into the systemic and carotid arches. The blood in the systemic arch is a mixture of that from the right and left auricles; the final portion which passes into the carotid comes only from the left auricle. The meaning of this separation of the blood will be seen later.

To and from the heart leads a complicated system of *blood vessels*, through which the red blood is driven by the heart-beat. The vessels which lead from the heart are called *arteries*; those which lead to the heart are *veins*. The arteries have thick, muscular walls, and after many subdivisions become small vessels known as *arterioles*. These in turn divide into minute, very thin-walled vessels called *capillaries*, which lie among the tissues in the form of a meshwork, which in active tissues, such as glands and muscles, is exceedingly fine, so that the blood is brought close to every part. From the capillaries the blood is collected into small

**Circulation of
the Blood.**

venules which join to form the veins. The walls of the veins are thinner and less muscular but more elastic than those of the arteries, and many of them contain small watch-pocket valves, placed with the opening of the pockets towards the heart so as to prevent the blood from being driven in the wrong direction when the vessels are compressed by the movements of the body. Through heart, arteries, capillaries, and veins there takes place a *circulation of the blood*, which can be seen under the microscope in the capillaries of the thin web between the toes of the frog's foot. In the arteries the blood flows fast and with jerks, which are caused by the beating of the heart and known as the *pulse*. In the arterioles the increased friction owing to the increased surface of the numerous branches obliterates the pulse. In the capillaries the increased area lessens the rate of flow. In the veins the blood is flowing back to the heart evenly and less fast than in the arteries, though faster than in the capillaries.

From the truncus arteriosus there arise on each side three

arteries, which are for some distance bound together, so that they seem to be a single vessel. The hindermost of these is the *pulmocutaneous arch*, the middle the *systemic arch*, the foremost the *carotid arch*. After separating, the three arches continue to run outwards, diverging as they go. The pulmocutaneous arch divides into the *pulmonary artery* for the lung and the *cutaneous artery* for the skin. The carotid arch gives off forwards a *lingual artery* to the muscles of the tongue and hyoid, and then becomes the *common carotid artery* which bears a round swelling due to the fact that it here breaks up into a number of small vessels which reunite. This swelling is the *carotid labyrinth*, often inappropriately called the *carotid gland*. The friction of the blood against the large surface

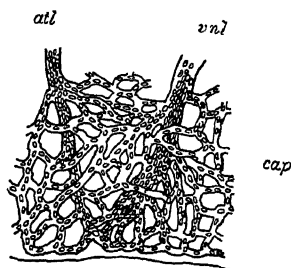


FIG. 29.—Capillaries in the web of a frog's foot.—After Allen Thomson

atl, Arteriole cap, capillaries, vnl, venule

provided by its numerous small vessels is the cause of the high pressure in the carotid arch

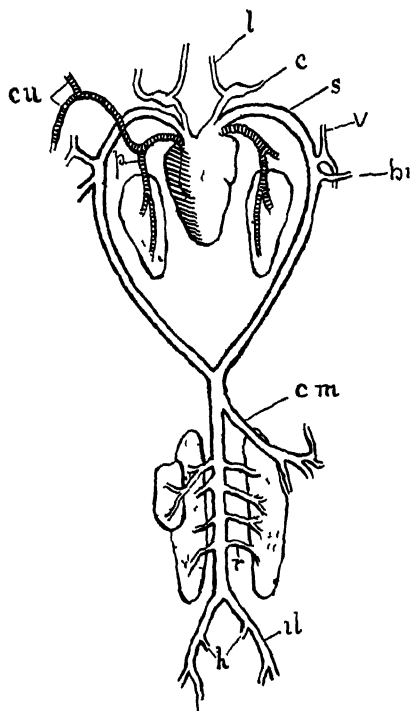


FIG 30 —A diagram of the arterial system of the frog, seen from the ventral side —
From Thomson

br, Subclavian or brachial, *c*, common carotid, *cm*, caeliaco mesenteric, *cu*, cutaneous artery, *l*, haemorrhoidal, *il*, common iliac, *l*, lingual artery, *p*, pulmonary, *r*, renal, *s*, systemic arch, *v*, occipito vertebral. The right spermatic artery is shown but not lettered

Beyond the carotid gland the artery runs forwards and upwards towards the head, where it divides into an *internal carotid*, which passes into the skull and supplies the brain, and an *external carotid*, which supplies the orbit and roof of the mouth. The systemic arch curves upwards and backwards round the oesophagus to join its fellow in the middle line below the backbone. On its way it gives off an *oesophageal artery* to the oesophagus, an *occipito vertebral artery* to the head and backbone, and a large *subclavian artery* to the arm. Just before joining its fellow, the left systemic arch gives off backwards the large *caeliaco mesenteric artery*. This divides

into an *anterior mesenteric* to bowel and spleen and a *caeliac*, which supplies the stomach after giving a *hepatic* branch to the liver. The vessel formed by the junction of the systemic arches

bular from the lower jaw. The innominate arises by the junction of an *internal jugular* from the head and a *subscapular* from the shoulder and back of the arm. The subclavian receives the *brachial* from the arm and the great *musculo-cutaneous* from the skin, the mucous membrane of the mouth, and many head and trunk muscles. The inferior vena cava arises by the junction of several *renal veins* from the kidneys and *ovarian or spermatic veins* from the generative organs, and, just before it enters the sinus, is joined by two *hepatic veins* from the liver. Blood is returned from the legs by a *femoral vein* on the outside and a *sciatic* on the inside of each limb. Each femoral vein divides on reaching the trunk into a *renal portal* and a *pelvic*. The former receives the sciatic and runs to the kidney, just before entering which it receives the *dorsolumbar vein* from some of the muscles of the back. In the kidney the vein breaks up into capillaries, which are collected, with those of the renal artery, to give rise to the renal veins. Thus it comes about that much of the blood in the renal veins has passed through two sets of capillaries, one in the leg and another in the kidney. Such an arrangement, in which the blood having passed through one set of capillaries is then sent through a second, is called a *portal system*. The pelvic veins of the two sides lie in the abdominal wall and join to form the *anterior abdominal vein* which runs forwards above the linea alba in the middle of the belly (sec p. 40). This vessel receives a small *vesical vein* from the bladder, several pairs of vessels from the recti muscles of the abdomen, and a little backward vessel from the heart. It ends in front by passing into the liver and there breaking up into capillaries again. The blood from the stomach, bowel, pancreas, and spleen is gathered up into a great *hepatic portal vein*, which also breaks up in the liver. Thus the liver has a portal system, which is fed with blood (*a*) from the dorsal aorta, (*b*) from the anterior abdominal vein, (*c*) from the hepatic portal vein, and discharges by the hepatic veins into the inferior vena cava.

The general course of the circulation in the frog is summed up in the table on the opposite page. The thick lines indicate venous blood, the narrow lines arterial blood.

Course of the
Circulation.

The elaborate arrangements whereby the blood circulates through all parts of the body point to the fact that it is a universal means of transport between them. It conveys nourishment from the gut to the rest of the body, bears oxygen from the organs of respiration to the tissues and the waste products of metabolism from the tissues to the organs of excretion,

Functions of the Blood

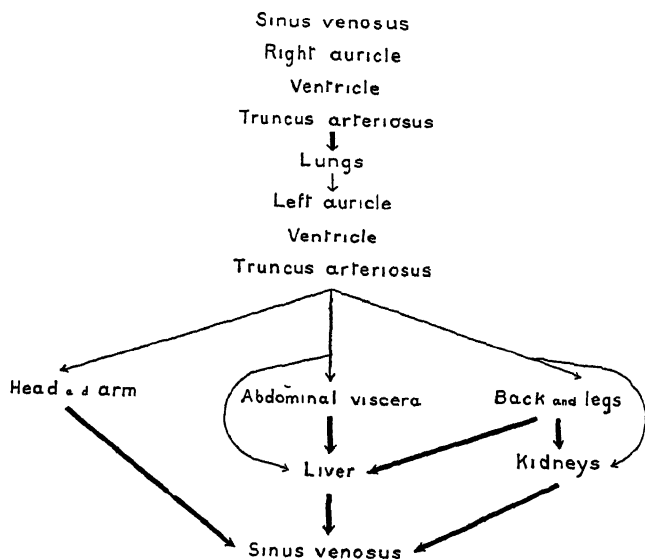


FIG. 32 —A diagram of the circulation of the blood in the frog
Thick lines indicate venous blood, narrow lines arterial

and carries various substances which are secreted into it by the liver and other organs to the regions of the body where they are made use of

The preceding paragraph must not be taken to indicate that the blood comes itself into contact with the tissues. The blood vessels are completely closed, and the tissues are actually bathed by another fluid, known as *lymph*, which is produced by exudation

Lymph

through the capillary walls. This fluid is gathered by small *lymphatic vessels* into the big *lymph sacs* already mentioned, whence it is pumped back into the veins by two pairs of small contractile sacs known as *lymph hearts*. One pair of these lies below the scapulæ and opens into the subscapular veins, the other lies at the end of the urostyle and opens into the femoral veins.

The *respiratory organs* of the frog are the *lungs*, the *skin*, and the mucous membrane of the *mouth*.

Organs of Respiration The lungs communicate with the pharynx by way of the glottis, which leads into a short, wide *windpipe* consisting of the *larynx* or *voice organ* only, without the long trachea, or windpipe proper, which is found in animals with necks. The walls of this cavity are supported by a pair of flat *arytenoid cartilages* and a very irregular ring, the *cricoid cartilage*. The lining of the larynx is thrown into a pair of folds, the *vocal chords*. Between these is a narrow slit, the *rima glottidis*, through which the air must pass to and from the lungs. The cartilages are supplied with muscles, by means of which they can be moved, so as to tighten the vocal chords and bring them close together. In this condition the chords vibrate when air from the lungs is forced between them, and produce a sound which is the croaking of the frog. From the hinder part of the windpipe an opening leads on each side to a short tube known as the *bronchus*, which begins at once to expand into the lung. The latter is a wide, thin-walled, elastic, highly vascular sac, whose internal surface is increased by being thrown into numerous folds. The lungs of the frog are not enclosed, like those of man, in a "chest" shut off by a midriff, but lie free in the forepart of the common body cavity, and the mode of breathing is correspondingly different in the two cases. In man, breathing is brought about by an enlargement of the chest, which draws air into it, followed by a collapse which drives it out. In the frog, air is drawn into the mouth by a lowering of the floor by the muscles of the hyoid, the nostrils being open and the mouth and glottis closed. The floor of the mouth is then raised by the mylohyoid and jaw muscles, while the glottis is open and the mouth and nostrils closed. The air is thus driven into the lungs, from which it is after

wards expelled by the collapse of their elastic walls, aided by contraction of the abdominal muscles

In the lungs an interchange of oxygen for carbon dioxide takes place through the thin walls between the air and the blood in the lung capillaries

Arterial and Venous Blood

The same process goes on in the very vascular mucous membrane of the mouth and in the skin. In the tissues of the body the blood undergoes a reverse change, parting with its oxygen to the protoplasm and receiving from it carbon dioxide. The blood which has thus become poor in oxygen and rich in carbon dioxide returns to the heart through the veins. Such blood is therefore known as *venous blood*. It is of a dark red colour. On reaching the heart, this blood is directed, as we have seen, principally to the lungs, skin, and mucous membrane of the mouth, there to be oxygenated again. The blood from the skin and mouth mingles on its way back to the heart with the venous blood, but that from the lungs returns separately to the heart and is then sent forth again to the tissues through the arteries. Oxygenated blood is therefore called *arterial*. It is of a bright red colour. It will be noted that the pulmonary artery contains venous blood the pulmonary vein arterial blood. It will also be seen that the course of the circulation contains two circuits, one short, passing through the lungs, and the other long, passing through the rest of the body, the blood returning to the heart between the two. This is shown in the Table on p. 59. The two circuits are known respectively as the *lesser or pulmonary* and the *greater or systemic* circulations.

The respiratory organs are engaged, as we have seen, in the excretion of carbon dioxide, and some water is also lost in the form of vapour through these organs. A further loss of water in a liquid form and the excretion of solids dissolved in it takes place through the *kidneys*. These are a pair of flattened, oblong, dark red bodies which lie one on each side in the dorsal lymph sac above the coelom and below the backbone. Each consists of a mass of twisted *uriniferous tubules*, held together by connective tissue and richly supplied with blood vessels. Each tubule begins blindly in the substance

Excretory Organs

vein The tubules open into *collecting tubes*, which run across the kidney to enter the main duct of the organ or *Wolffian duct*¹ This lies along the outer edge of the organ and passes backward to open into the dorsal side of the cloaca Water is excreted in the glomeruli, and solids, chiefly urea, in the glandular part of the tubules The urine is held in the bladder and voided at intervals

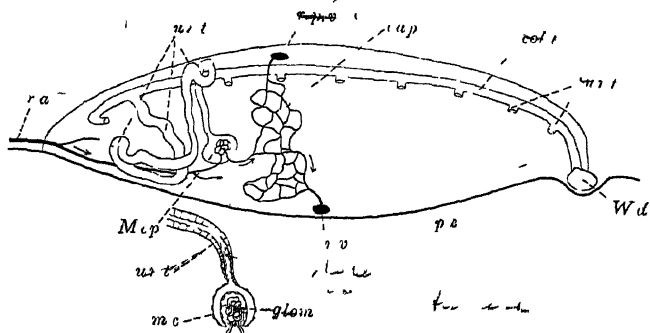


FIG 34—A diagram of a kidney of the frog, to show the arrangement of the tubules and blood vessels One uriniferous tubule and a portion of the vascular meshwork are shown separately In reality the blood vessels entangle the tubules

cap, Capillaries colt, collecting tubule glom, glomerulus, Mcp, Malpighian capsule mc, the same more highly magnified, pc, peritoneum ra, renal artery, rpv, branch of the renal portal vein, rv, branch of a renal vein urt, uriniferous tubule urt places where other uriniferous tubules open into the collecting duct, Wd, Wolffian or kidney duct

The organs in which the ova and spermatozoa of animals are formed are known as *gonads* Those in which spermatozoa arise are *testes*, those in which ova arise are *ovaries* The male organs of reproduction of the frog are the testes and their ducts The testes are a pair of ovoid bodies slung from the surface of the kidneys by a fold of the peritoneum known as the *mesorchium* Each consists of a mass of *seminiferous tubules*, in which the spermatozoa are formed They communicate by about half a dozen small ducts, the

¹ Often called the ureter, although it does not correspond with the ureter of man



FIG 35 —The urinary and genital organs of a female frog

aav, Anterior abdominal vein, cut short and turned back, *bl*, urinary bladder, *cl*, cloaca, *es*, egg sac, *fb*, fat body, *fv*, femoral vein, *iod*, internal opening of oviduct, *ivc*, inferior vena cava, *k*, kidney, *kd*, Wolffian or kidney duct, *od*, oviduct, *ovv*, left ovary, *orv*, ovarian vein, *plv*, pelvic vein, *rl*, right lung, *rv*, renal vein, *rpv*, renal portal vein, *scv*, sciatic vein, *srb*, adrenal body. The ovary and fat body of the right side have been removed.

vasa efferentia, in the mesorchium, with the collecting tubules of the kidney, along which, and through the Wolffian ducts, the sperm passes to the cloaca, the frog having no independent kidney duct. In the male each Wolffian duct has attached to it a sac, the *vesicula seminalis*, in which the sperm is stored until it is used for fertilising the eggs of the female. In the female the ovaries correspond in position to the testes, the membrane by which each of them is slung being known as the *mesovarium*. They are pleated folds of peritoneum containing eggs in various stages of ripeness held together by connective tissue. In the breeding season they increase in size and shed the ripe eggs into the body cavity, where, in some way not understood, the eggs find their way into the internal openings of the *oviducts*. These are long twisted tubes, one on each side of the body, opening in front into the body cavity by a small aperture at the base of the lung, and behind into the cloaca just before the opening of the Wolffian ducts. The greater part of each tube is narrow and glandular and secretes a slimy substance, which sets into a jelly on coming into contact with water, but at the hinder end the duct enlarges into a sac, which at the breeding season becomes distended with eggs and occupies a great part of the body cavity. At this season, which is in March, the male mounts upon the back of the female, clasping her behind the arms with his fore limbs, which are provided for the purpose with the pads we have already mentioned. In this position the animals remain for days until the eggs are laid. As the spawn passes out, the male pours his sperm over it, the eggs are fertilised, and the slimy coating they have acquired in the oviduct swells up and sets in the water so as to form a protective layer of jelly.

CHAPTER IV

THE FROG: NERVOUS SYSTEM AND SENSE ORGANS

IN the nervous system of the frog there may be recognised two main parts—the *cerebro-spinal system*, connected with the organs of sense and the voluntary muscles, and the *sympathetic or autonomic system*, connected with the viscera and blood vessels. The cerebro-spinal system comprises the *central nervous system or cerebro-spinal axis*, composed of the brain and the spinal cord, and the *peripheral nervous system*, containing the *cerebro-spinal nerves* and certain knots of nerve cells upon them, known as their *ganglia*. There are ten pairs of *cranial nerves* arising from the brain, and the same number of *spinal nerves*. The sympathetic system also consists of nerves and ganglia.

The spinal cord is an elongated, subcylindrical structure, lying in the vertebral canal of the backbone. It is somewhat flattened from above downward, tapers to a fine thread, the *filum terminale*, in the urostyle, and swells somewhat in the regions of the limbs. A transverse section (Fig. 57) reveals the fact that it is traversed by a *central canal*, which ends blindly behind, but in front is continuous with cavities in the brain. It is composed of nervous tissue enclosed in a connective tissue sheath, the *pia mater*, which, along the dorsal and ventral middle lines, passes in to some depth as the *dorsal and ventral fissures*. The nervous tissue is of two kinds, a *white matter* outside and a *grey matter* around the central canal. In transverse section the grey matter extends as *dorsal and ventral horns* on each side.

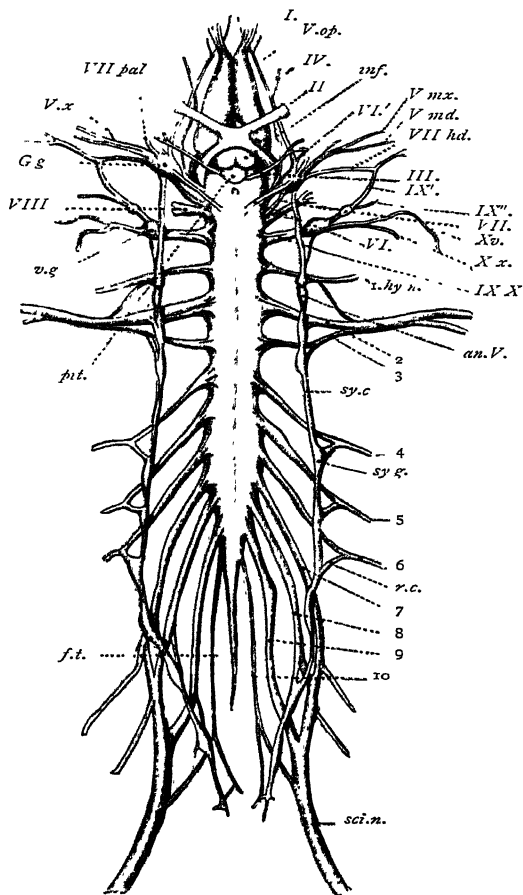


FIG. 36.—The central nervous system and principal nerves of a frog, seen from below.—Modified, after Ecker.

I.-X., Cranial nerves; 1-10, spinal nerves; *V.md.*, *V.mx.*, *V.op.*, mandibular, maxillary, and ophthalmic branches of fifth cranial nerve; *VI.*, sixth cranial nerve after leaving the Gasserian ganglion; *VII.hd.*, *VII.pal.*, hyoidean and palatine branches of seventh cranial nerve; *IX'*, branch from ninth cranial nerve to seventh; *IX''*, main branch of ninth cranial nerve; *IX'''*, tenth cranial nerve passing to viscera; *V.x.*, a small twig from the undivided main branch of the fifth cranial nerve; *X.x.*, a branch from the vagus to certain muscles; *an.V.*, annulus of Vieussens through which the subclavian artery passes; *f.t.*, filum terminale; *G.g.*, Gasserian ganglion, *hy.n.*, hypoglossal (first spinal) nerve; *inf.*, infundibulum; *pit.*, pituitary body; *r.c.*, ramus communicans; *sci.n.*, sciatic nerve; *sy.c.*, longitudinal commissure of sympathetic chain, *sy.g.*, sympathetic ganglion; *v.g.*, vagus ganglion.

The ten pairs of spinal nerves pass out between the vertebrae to be distributed over the body

Spinal Nerves

Each nerve is surrounded as it issues by a soft, white *calcareous concretion*. Every nerve arises by two roots, a dorsal and a ventral, and the dorsal root bears a small swelling, the *dorsal root ganglion*. Just outside the back bone the two roots join, and the nerve thus formed proceeds at once to divide, giving rise to (a) a short *dorsal branch* to the muscles and skin of the back, (b) a long and conspicuous *ventral branch* to the muscles and skin of the sides and ventral surface of the trunk, and in some

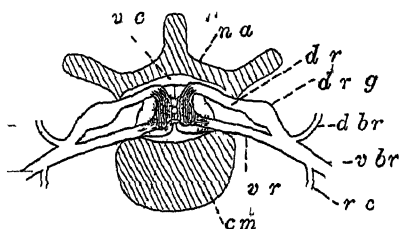


FIG 37—A diagram of the origin of the spinal nerves of the frog

cm, Centrum *dbr*, dorsal branch of the nerve
dr, dorsal root *drg*, dorsal root ganglion
na, neural arch *rc*, ramus communicans
vbr, ventral branch *vc*, vertebral canal
vr, ventral root

cases to the limbs, and (c) a small *ramus communicans* to the sympathetic system

The dorsal root is also called *sensory or afferent* because along it impulses pass inwards to the spinal cord and produce, among other effects, "sensation," and the ventral is called *similarly motor or efferent* because along it

impulses pass outward and produce, among other effects, contraction of muscles. This is shown by the fact that cutting the dorsal root deprives the parts supplied by its nerve of sensation, while cutting the ventral root paralyses the same parts. Each of the branches contains elements derived from both dorsal and ventral roots. The course of the dorsal branches and rami communicantes is much the same in all cases, but that of the ventral branches differs greatly in different nerves and must now be followed

The *first spinal nerve*¹ is known as the *hypoglossal*

¹ The nerve which is counted as the first spinal nerve in the frog is in reality the second. The true first spinal nerve, which should issue between the skull and the first vertebra, appears in the embryo, but is lost later on.

It leaves the neural canal between the first and second vertebræ, curves round the throat, turns forward below the mouth, and proceeds to the tongue. The *second spinal nerve* is a large strand running straight outwards. It receives branches from the first and third, forming thus the *brachial plexus*, and proceeds as the *brachial nerve* to the arm. The *third spinal nerve* is small, and beyond the brachial plexus resembles the *fourth, fifth, and sixth spinal nerves*. All these are small and run backwards to supply the muscles and skin of the belly. The *seventh, eighth, ninth, and tenth spinal nerves* join to form a *sciatic plexus*, from which arise several nerves to the hind-limb, the principal being the very large *sciatic nerve*. The tenth nerve leaves the vertebral canal by a foramen in the side of the urostyle. The roots of the last four pairs of nerves do not issue from the spinal canal at once, but run backwards for some distance from their origin to reach their point of exit. Thus, they form inside the vertebral canal a bundle known as the *cauda equina*.

The brain may be divided into three regions, known respectively as the *hind, mid, and fore brains*.

Brain.

The hind-brain consists of the *medulla oblongata* and the *cerebellum*. The medulla oblongata is the hindermost part of the brain. It is continuous behind with the spinal cord, which, as it is traced into the brain, widens, the central canal enlarging into a cavity in the medulla known as the *fourth ventricle* of the brain, the ventral side thickening, and the dorsal thinning out into a slight membrane over the fourth ventricle. The pia mater above this membrane is very vascular and thrown into folds which project into the ventricle, forming thus a structure known as the *posterior choroid plexus*. The cerebellum is a narrow band across the roof of the front part of the fourth ventricle. In many other animals it is relatively much larger. The *mid-brain* is the region in front of the medulla. It has a thick floor formed by two longitudinal columns known as the *crura cerebri*, a roof consisting of a pair of rounded swellings known as the *optic lobes*, and internally a narrow passage, the *aqueduct of Sylvius*, continuous behind with the fourth ventricle and above with cavities in the optic lobes. The fore-brain consists of the *thalamen-*

cephalon and the *cerebral hemispheres*. The thalamencephalon lies immediately in front of the mid-brain. Its sides are thick and are known as the *optic thalami*; its roof and floor are thin. The floor is prolonged into a hollow structure known as the *infundibulum*, to the end of which is applied a glandular, non-nervous mass called the *pituitary body* or *hypophysis*. The roof is prolonged into a

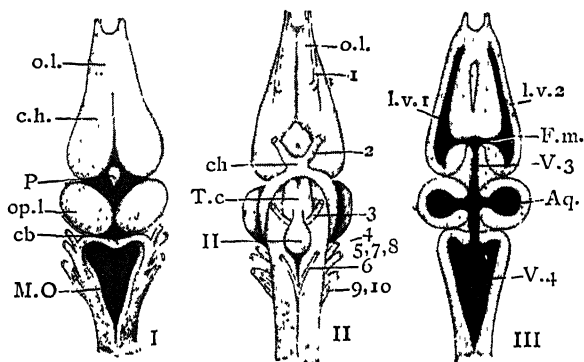


FIG. 38.—The brain of a frog.—After Wiedersheim.

- I. DORSAL ASPECT.—*o.l.*, Olfactory lobes; *c.h.*, cerebral hemispheres, *P.*, pineal stalk, rising from region of optic thalamus, *op.l.*, optic lobes; *cb.*, rudimentary cerebellum, *M.O.*, medulla oblongata.
- II. VENTRAL ASPECT.—The numbers indicate the origins of the nerves. *ch.*, Optic chiasma; *T.c.*, tuber cinereum (infundibulum); *II.*, pituitary body or hypophysis.
- III. HORIZONTAL SECTION.—*l.v.* 1 and 2, lateral ventricles of cerebrum; *F.m.*, foramen of Monro, *V.* 3 and 4, third and fourth ventricles; *Aq.*, cavities of optic lobes and aqueduct of Sylvius from third to fourth ventricle.

short, hollow stalk, which in the tadpole is connected with a structure known as the *pineal body*. In the adult this has become separated and lies outside the skull. In certain other animals the pineal body is much more highly developed and still connected with its stalk, and its structure shows that it is the remnant of a middle eye, though it is no longer functional. In front of the pineal stalk lies an *anterior choroid plexus*. The cavity of the thalamencephalon is deep but narrow, and is known as the *third ventricle*. It is bounded in front by a wall known as

the *lamina terminalis*. Behind this on each side an opening known as the *foramen of Monro* leads into the cavity or *lateral ventricle* of one of the cerebral hemispheres. These are oblong oval bodies narrowing forwards to join a mass which is indistinctly separated into two *olfactory lobes*. The median walls of the cerebral hemispheres touch in front and behind, but for a considerable distance they are quite separate. The brain, like the spinal cord, contains both white and grey matter. In the medulla oblongata and optic lobes the grey matter lies mainly around the ventricles, but in the thalamencephalon, cerebral hemispheres, and olfactory lobes there is an outer grey layer or *cortex* over the white matter.

The *first or olfactory cranial nerve* of each side arises from the olfactory lobe and runs forward to the olfactory organ in the nostril. The *second or optic nerve* starts from the side of the mid-brain, curves round underneath the brain, running forwards and inwards, and crosses its fellow below the thalamencephalon on its way to the eyeball of the opposite side. Where the nerves cross they are fused, and the X shaped structure thus formed is called the *optic chiasma*.² The *third or oculomotor nerve* supplies the eye muscles, with the exception of the superior oblique and external rectus. The small *fourth, pathetic, or trochlear nerve* arises between the optic lobe and cerebellum and supplies the superior oblique muscle. It is the only nerve which starts from the dorsal surface of the brain. The large *fifth or trigeminal nerve* arises from the side of the anterior end of the medulla. Just before it passes through its foramen it bears a large swelling, the *Gasserian ganglion*. It then divides at once into an *ophthalmic branch*, which runs forwards along the inner wall of the orbit and supplies the skin of the forepart of the head, and a *main branch*, which runs outwards across the hinder part of the orbit and divides into a *maxillary branch* to the upper jaw and a *mandibular branch* to the lower jaw.

¹ For the foramina by which the cranial nerves leave the skull, see p. 31. These nerves can more easily be dissected in the dogfish, where their course is substantially the same (see pp. 303-305).

² The crossing is not complete, part of each nerve proceeding in that limb of the X which passes to the eye of the same side.

The *sixth or abducent nerve* is very small. It arises from the ventral side of the medulla about the middle of the length of the latter, and supplies the external oblique muscle, after passing through the Gasserian ganglion. The *seventh or facial nerve* arises from the side of the medulla behind the fifth. It joins the Gasserian ganglion.¹ On leaving this it at once divides into a *palatine branch*, which runs forwards on the floor of the orbit to supply

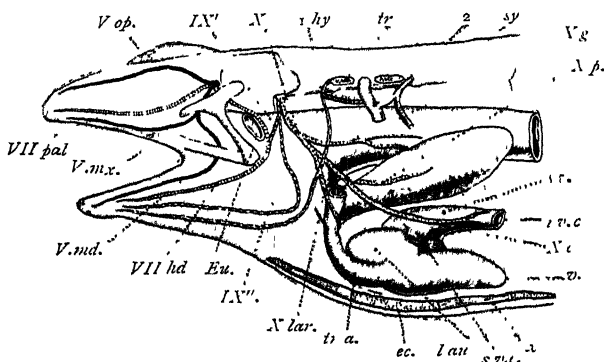


FIG. 39.—A diagram of a dissection, from the left side, of the forepart of the body of a frog.—Partly after Marshall.

V.-V', Cranial nerves; V.md., V.mx., V.op., mandibular, maxillary, and ophthalmic branches of fifth cranial nerve; VII.hd, VII.pal, hyoid and palatine branches of seventh cranial nerve; IX', branch of ninth cranial nerve to seventh; IX'', main branch of ninth cranial nerve; X.c., X.g., X.lar., X.p., cardiac, gastric, laryngeal, and pulmonary branches of tenth cranial nerve; 1, 2, spinal nerves; ec., epicoracoid; Eu., Eustachian tube; hy., hypoglossal; i.v.c., inferior vena cava; l.au., left auricle, s.v., sinus venosus; s.v.c., left superior vena cava; sy., sympathetic chain, tr., transverse process of second vertebra; tr.a., truncus arteriosus, v., ventricle; x., xiphisternum

the roof of the mouth, and a *hyomandibular branch*, which runs outwards and supplies the muscles of the hyoid and the lower jaw. The *eighth, auditory, or acoustic nerve* arises from the side of the medulla with the seventh, enters the auditory capsule, and ends in the membranous labyrinth of the ear. The *ninth or glossopharyngeal nerve* arises from the side of

¹ This ganglion is formed by the fusion of two ganglia which are distinct in the tadpole. One is the true Gasserian ganglion and belongs to the fifth nerve; the other is the *geniculate ganglion* and belongs to the seventh.

the medulla behind the eighth, immediately joins the tenth nerve, and passes through the ganglion of the latter. It then bears a small ganglion of its own, gives a branch to join the hyomandibular nerve, and proceeds round the throat to turn forward and run along the floor of the mouth, supplying various structures there. The *tenth or vagus nerve* is large and very important. It arises by several roots adjoining the ninth, with which it is fused as far as the *vagus ganglion*. It then turns backward and downward round the throat and gives branches to the larynx, heart, lung, and stomach.

The cranial nerves do not, like the spinal nerves, arise each by a sensory and a motor root, but it is possible to distinguish among them a purely sensory series, a purely motor series, and a series of mixed function. The tenth, ninth, seventh, and fifth nerves are *mixed*. They correspond to the dorsal roots of spinal nerves with the addition of that part of the ventral root which passes by the *rami communicantes* to the sympathetic system. This part in the cranial nerves passes direct to the alimentary canal and vascular system. Each of the mixed nerves retains its dorsal root ganglion as a member of the series formed by the Gasserian, geniculate, auditory, glossopharyngeal, and vagus ganglia. The sixth, fourth, and third nerves are purely *motor* and correspond to the ventral roots of spinal nerves, the sixth being the ventral root of the seventh, the fourth that of the fifth, and the third that of a nerve whose dorsal root is contained in the ophthalmic nerve. The eighth is purely *sensory* and represents part of a dorsal root. Its ganglion is embedded in the labyrinth of the ear. The second and first nerves are also purely sensory, but are not comparable to the dorsal roots of spinal nerves.

The sympathetic system consists of a long nerve on each side of the body below the backbone and along side the aorta and systemic arch. It is connected by a *ramus communicans* with each spinal nerve. At the junction of each *ramus communicans* the sympathetic cord swells into a *ganglion*. In front the longitudinal cord enters the skull with the ninth and tenth nerves, is connected with the tenth, and ends in the

Gasserian ganglion. From the sympathetic ganglia small nerves are given off to those of the opposite cord and to the blood vessels and viscera. These nerves break up, join, and rejoin to form networks or *plexuses*.

If any nerve be traced outward from the central nervous system, it is found, after dividing into finer and finer branches, to end by entering some organ. Here the fine fibres of which every nerve is composed (see p. 92) end by coming into connection with the cells of various tissues. Efferent fibres (*i.e.* those derived from the ventral root) join muscular tissue, which the impulses they conduct will cause to contract, or glandular tissue, which their impulses will cause to secrete. Afferent fibres (*i.e.* those which pass through the dorsal root or one of the sensory cranial nerves) come into relation with cells of various kinds which are especially irritable by some kind of stimulus (as those of the lining of the eye by light), and their function is to conduct to the central nervous system impulses set up by these stimuli. Thus we may sum up the arrangement of the nervous system by saying that it consists of a central mass and a series of afferent and efferent paths along which impulses pass to and from it.

It will be clear from the arrangement of the nervous system which we have just described that it is a complicated apparatus for conveying messages between the different parts of the body through the intervention of a central exchange. In it conductivity is highly developed, as irritability is in the sense organs; its arrangement, however, is such that impulses are carried, not directly from organ to organ, but from each organ to the central nervous system, whence, if action is to take place, fresh impulses are directed to other organs. It is by the intervention of the central nervous system that there take place in an orderly manner the very complex responses which the simplest stimuli evoke in the body of one of the higher animals. Even such slight and passing actions, for instance, as a leap from danger or the snapping up of an insect involve the harmonious action of numerous muscles in a manner which would be impossible without some co-ordinating mechanism.

**Functions of
Nerves in
General.**

**Physiology of
the Nervous
System.**

The actions which are excited through the nervous system are of two kinds, reflex and voluntary. A *reflex action* is one in which stimulation of an afferent nerve brings about through an efferent nerve the production of activity in some tissue in an involuntary manner. Thus touching the eye brings about contraction of the muscle of the eyelid so that blinking takes place, but this happens without any effort of the will of the animal, which exercises no choice as to whether it shall take place or not. In a reflex action the same stimulus is always followed by the same response. In blinking the action is conscious, but many reflex actions are purely unconscious,

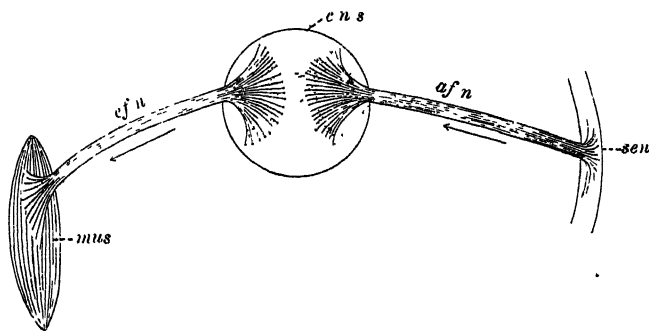


FIG. 40.—A diagram of the "reflex arc."

af.n., Afferent nerve; *c.n.s.*, central nervous system; *ef.n.*, efferent nerve, *mus.*, muscle; *sen*, sensory surface.

as when the passage of food over the opening of the bile-duct causes through the central nervous system a discharge of bile from the gall-bladder without either the will or the knowledge of the animal. For a reflex action three things are necessary: (1) an afferent nerve, (2) a portion of the central nervous system, known as the *centre* of the reflex, (3) an efferent nerve. This apparatus is known as the *reflex arc*. For some reflex actions the centre is in the brain, but for many it is only necessary that a part of the spinal cord should be intact. Thus a frog from which the brain has been removed will lift its leg to wipe off an irritant, such as a drop of acid, from its flank. A *voluntary action* is one in which the will intervenes, and a choice is made, as when

the animal decides between two directions in which it can escape an enemy, or seeks food because it is hungry. Voluntary actions may or may not follow immediately upon an external stimulus, but when they do so the same stimulus is not always followed by the same response. However the action be started, its nature is determined anew in each case. For nearly all, if not for all, voluntary actions it is necessary that some part of the cerebral hemispheres should be uninjured.

In the last paragraph we have had to mention *consciousness* as accompanying certain events in the nervous system. A conscious being is one that is aware of events. The events of which it is immediately aware take place in its own body. Awareness of external events is of course due to awareness of internal events which they cause.¹ A vast number of events in the human body are accompanied by consciousness, but no event is so accompanied unless it affect the nervous system. On the other hand, the opening of the bile-duct which we mentioned above is but one of innumerable events involving the nervous system which take place in the viscera and elsewhere quite unconsciously. It is, of course, impossible for us to be certain that a frog possesses consciousness, but just as each of us infers from the behaviour of other men that they have a consciousness like his own, so it may be inferred from the behaviour of the frog that it possesses some dim counterpart of the consciousness of mankind. An unsolved and perhaps insoluble problem is presented by the relation of consciousness to the events which it pictures. Is it caused by them? Does it affect their course? These are, of course, questions of the highest importance to philosophy. All that need be said here is that, though the consciousness of the living organism is probably always accompanied with events in the nervous system, the

¹ This is not to say that the conscious being knows that the events of which it is aware are in the first place only events within itself. Ordinarily, the processes in sense organs and nervous system are not regarded, and consciousness is accepted as first-hand evidence of external things. Still less is it realised that consciousness does not necessarily bear the likeness of things outside it, not even of the bodies with whose working it is linked, but rather signs which stand for such things, and that after this fashion alone does it know material things.

legitimate inference from this is, not that either of them is the cause of the other, but rather that between them there is some relation whose nature is unknown to us. We are here dealing with two things of wholly different kinds, the events which happen in the nervous system being physical¹ processes and consciousness a psychical process, and we can no more expect to understand consciousness from a study of the brain than we could imagine a ray of light to see itself.

The senses of a backboned animal, such as a frog, are more numerous than is generally realised. Besides the "five senses" of sight, hearing, smell, taste, and touch, there are distinct kinds of sensibility to heat, cold, and the movements of the body, and an indefinite "general sensibility" which when it is slight produces such sensations as tickling, but when it becomes excessive rises into pain. Each of these senses has origin in impulses derived from a special kind of nerve ending, but only in the case of sight, hearing, and smell are these endings situated in a highly specialised organ. We shall here consider only these organs.

The eyeball of the frog is roughly spherical, but flattened on the front side. It consists of the following parts: (1) The *outer coat or sense capsule* corresponds to the auditory and nasal capsules, but fits closely to the eye instead of forming a hollow capsule fused to the skull. Over the greater part of the eye it consists of dense connective tissue with some cartilage and is known as the *sclerotic*, but on the front

Sense Organs
General State
ments

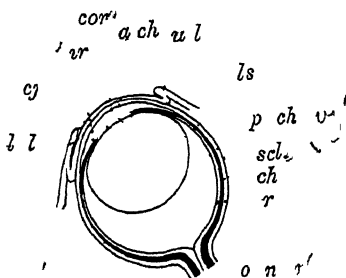


FIG. 41 — A diagram of a section through the eye of a frog

a ch Anterior chamber *ch*, choroid *c j* conjunctiva *cor*, cornea *u l* iris *ls* lens *l l* lower lid *o n*, optic nerve, *p ch*, posterior chamber *r*, retina, *scl*, sclerotic, *u l*, upper lid

¹ That is, processes which go on in material bodies, not necessarily "physical" in the sense in which that term is opposed to "chemical"

side it is transparent and known as the *cornea*. (2) The skin over the cornea adheres to it as a very delicate and transparent covering called the *conjunctiva*, which is kept moist by the secretion of glands below the eye. (3) Inside the sense capsule is the *choroid coat*, consisting of looser and highly vascular connective tissue containing numerous dark pigment cells. In front the choroid separates from the sclerotic and passes inwards, as a partition called the *iris*, across the hollow of the eyeball, which it thus divides into

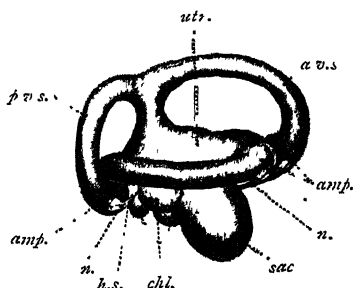


FIG. 42.—The labyrinth of the right ear of the frog, seen from the outer side.
—Partly after Marshall.

a v.s., Anterior vertical semicircular canal; *amp.*, ampullae, *chl.*, small dilations of the sacculus which represent the cochlea of higher animals; *h.s.*, horizontal semicircular canal; *n.*, branches of the auditory nerve to supply the ampullae; *p v.s.*, posterior vertical semicircular canal; *sac.*, sacculus, *utr.*, utricle.

anterior and posterior chambers. The former is smaller and filled with a watery *aqueous humour*, the latter larger and filled with a gelatinous *vitreous humour*. In the middle of the iris is an opening, the *pupil*, and the iris contains muscular tissue by which the size of the pupil can be altered.

(4) Immediately behind the iris lies a firm, transparent, subspherical body, the *lens*, which serves to focus upon the sensitive surface at the back of the eye the light which enters through the pupil. (5) The sensitive

surface is provided by the *retina*, a delicate membrane containing two primary layers, an outer *pigment layer* of pigmented cells lining the choroid, and an inner *retina proper* which has at the back of the eye a very complicated structure and is connected with the optic nerve, by which the impulses which give rise to sight are conveyed to the brain. The fibres of the optic nerve pass right through the retina and spread out over its inner surface (that which is turned towards the hollow of the eyeball). The percipient cells are on the outer surface, against the pigment layer, so that light must pass through

the layer of nerve fibres to reach them (Fig. 48, B). In the front half of the eye the retina loses its complicated structure and becomes very thin, but it continues to line the posterior chamber up to the edge of the pupil.

The essential part of the ear is the *membranous labyrinth* which we have already mentioned (pp. 31, 32).

Ears. It lies in the cavity of the auditory capsule. This cavity contains a fluid known as *perilymph*, and the membranous labyrinth contains a fluid known as *endolymph*. The labyrinth consists of the *vestibule* and the *semicircular canals*. The vestibule has an upper, larger division, the *utricle*, and a lower, smaller *sacculus*. From the former arise the three semicircular canals, which are arched tubes opening into the utricle at both ends. They are placed in planes at right angles to one another, one of them being *horizontal*, another longitudinal-vertical (the *posterior vertical*), and another transverse-vertical (the *anterior vertical*). One of the ends of each of them is enlarged to form a small, rounded *ampulla*. From the sacculus arise three small dilatations which represent the *cochlea* of higher animals. Between the auditory capsules and the *membrane of the ear-drum or tympanic membrane* on the side of the head lies the *cavity of the ear-drum or tympanic cavity*, which, as we have seen, is crossed by the *columella* from the *fenestra ovalis* to the tympanic membrane and communicates with the pharynx by the *Eustachian tube*. This region is called the *middle ear*, the labyrinth being the *inner ear*. There is *no outer ear* in the frog.

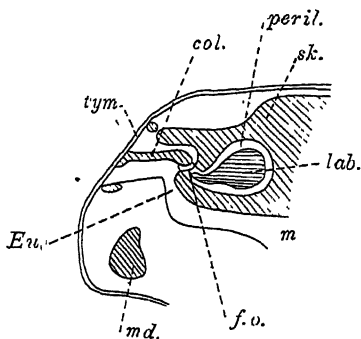


FIG. 43.—A diagram of the ear of the frog.

col., Columella; *f.o.*, fenestra ovalis; *Eu.*, Eustachian tube; *lab.*, part of the membranous labyrinth, containing endolymph; *m.*, mouth; *md.*, mandible; *peril.*, perilymph; *sk.*, skull; *tym.*, tympanic membrane.

From the sacculus arise three small dilatations which represent the *cochlea* of higher animals. Between the auditory capsules and the *membrane of the ear-drum or tympanic membrane* on the side of the head lies the *cavity of the ear-drum or tympanic cavity*, which, as we have seen, is crossed by the *columella* from the *fenestra ovalis* to the tympanic membrane and communicates with the pharynx by the *Eustachian tube*. This region is called the *middle ear*, the labyrinth being the *inner ear*. There is *no outer ear* in the frog.

The semicircular canals are not organs of hearing, but

enable the animal to keep its balance by judging the position of its head. Placed as they are in three planes of space, the fluid in them is set in movement by any change in position, and the differences in pressure on their walls which are thus brought about start impulses which the auditory nerve conveys to the brain. When they are diseased or injured giddiness is caused. The true organ of hearing is the sacculus. The vibrations which constitute sound set the tympanic membrane in motion, and its movements are transferred by the columella to the membrane of the fenestra ovalis and thence through the perilymph and the wall of the membranous labyrinth to the endolymph, where they stimulate the endings of the auditory nerve in the dilatations of the sacculæ.

Functions of the Ears. The organs of smell are a pair of irregular chambers, enclosed by the nasal capsules and communicating with the exterior by the nostrils and with the mouth by the *internal nares*. The lining of each is connected with the olfactory nerve of its side. Air is drawn through the chambers in the process of breathing, and the odorous particles it contains affect the cells of the lining which are connected with fibres of the nerve.

**Olfactory
Organs.**

CHAPTER V

THE FROG: HISTOLOGY, DEATH

THE study of tissues is a branch of anatomy known as *Histology*. It was shown in the first chapter
Histology : that the tissues of the animal body consist of
Cells. *protoplasm* accompanied in many cases by a *ground-substance* which supports it. The differences between tissues depend upon differences in arrangement and composition both of the protoplasm and of the ground-substance. When protoplasm is stained with certain dyes, portions of it colour more readily and deeply than the rest. These portions are usually collected into minute masses known as *nuclei*. The matter of which the nuclei are composed is known as *nucleoplasm*, the rest of the protoplasm as *cytoplasm*. In most tissues¹ the protoplasm is arranged in the little divisions, known as cells, to which we have already alluded, each cell containing one or a few nuclei and being of a size and shape peculiar to the tissue to which it belongs. The cells may either lie side by side (Fig. 5, C) or be separated by ground-substance (Fig. 5, B) or by a space filled with fluid (Fig. 63). Every cell arises by fission from another cell, grows, and behaves to some extent as an independent individual, but in the majority of cases it remains in connection with its neighbours by fine strands of protoplasm. A cell with more than one nucleus is a *multinucleate cell or cœnocyte*.

Either, as usually, in compact nuclei, or else scattered
Nuclei. through its substance, protoplasm always contains nucleoplasm, and it has been experimentally proved, by operations under the microscope in which the nucleus is removed from the cytoplasm, that nucleoplasm is

¹ In all the tissues of the frog.

necessary to the continuance of life. Without it many vital processes, such as fission—which is always preceded by division of the nucleus—assimilation, and secretion, are impossible, and life soon comes to an end. From these and other facts it appears that the nucleus has a regulative action over the life of the protoplasm. But the nucleus is no more capable of life apart from the cytoplasm than the latter can live without nucleoplasm. Thus the unit of living matter is a portion of nucleoplasm with its accompanying cytoplasm. Such a unit is known as an *energid*. A cell is an energid

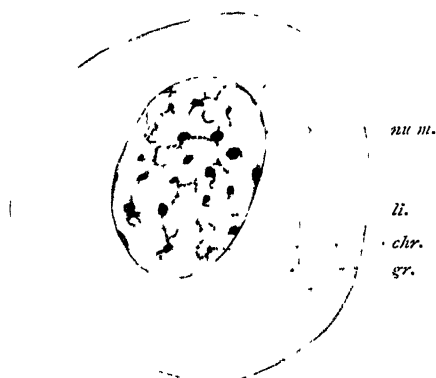


FIG. 44.—A diagram of a cell.

chr., Chromatin granules; *gr.*, granules in cytoplasm, *li.*, linin meshwork of nucleus; *nu. m.*, nuclear membrane.

which is in some way separated from the rest of the protoplasm of the body. A coenocyte is a group of energids.

Protoplasm itself has a fine *structure* which varies from tissue to tissue. Under high powers of the microscope it sometimes appears homogeneous, but usually as a meshwork of varying form composed of a somewhat denser substance known as *spongioplasm* with a more fluid *hyaloplasm* in its interstices.¹ Both these

¹ This appearance is interpreted in various ways. It is probably due, at least in some cases, to the fact that such protoplasm is a foam

substances are liquids containing various substances in solution and others in suspension as granules and droplets. Of the *chemical composition* of these solutions only the broad outlines are known, since it is not possible to analyse protoplasm without killing it and thereby bringing about in it chemical changes. The solvent is water, and in dead protoplasm the dissolved substances are in part inorganic salts, such as the phosphates and chlorides of sodium, potassium, and calcium, but principally organic compounds. Some of these, such as glycogen and organic compounds of ammonia, are comparatively simple and were probably in course of assimilation or excretion by the living substance, but the greater part are proteins, which are peculiar to protoplasm and never found except in it or in substances manufactured by it.¹ Metabolism never occurs without proteins, and its peculiar features certainly depend largely upon the nature of these substances, but it must not be overlooked that metabolism is exhibited only when the proteins form part of protoplasm, and only during the life of the latter. The granules and droplets suspended in protoplasm vary in composition and function. Some of them are truly alive. They are probably of the same nature as the spongioplasm but denser. Others, which may consist of proteins, carbohydrates, or fats, are to be regarded as material removed, for a time at least, from metabolism. Among the most important of them are certain granules which are revealed in the substance² of the meshwork of nucleoplasm by staining. They consist of a kind of matter known as *chromatin* from the fact that by its affinity for certain dyes it is the cause of the deep staining

or emulsion, the walls of whose bubbles are formed by the spongioplasm while the hyaloplasm fills them. These minute bubbles must not be confused with the larger spaces known as vacuoles (see below). The spongioplasm may contain threads of a substance still denser than the rest of it, lying in the walls of the bubbles, and some theories suppose that the whole of the spongioplasm has the form of threads.

¹ It is probable that during life the composition of protoplasm is much more complex than that which we have outlined, and that many of the bodies which can be obtained from dead protoplasm are in life united in loose compounds.

² Known as *linin*.

of the nucleus.¹ Besides these bodies, protoplasm often contains relatively large spaces filled with fluid known as *vacuoles*.

Protoplasm is extremely sensitive to the action of external agents, from which it is carefully screened in the bodies of most animals. Distilled water, solutions of salts, acids, alkalies, and narcotics all have characteristic effects upon it, stimulating, inhibiting, or killing it according to their nature and strength. It is also easily stimulated by electric shocks.

Reactions of Protoplasm.

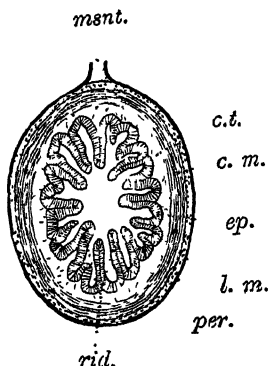


FIG. 45.—A diagram of a transverse section through the ileum of the frog.

c.m., Circular muscle layer; *c.t.*, connective tissue; *ep.*, epithelium which lines the gut; *l.m.*, longitudinal muscle layer; *mesent.*, mesentery; *per.*, peritoneum; *rid.*, longitudinal ridges of ileum.

Changes of temperature have marked effects upon it. Moderate heat acts as a stimulus, causing increased activity of movements, etc.; cold has a depressing effect. Heating above about 45° C. kills the protoplasm by causing its proteids to set into a solid mass or "coagulate." Cold below 0° C. stops all exhibition of life, but unless it is extreme does not prevent the reappearance of vital processes if the temperature be raised.

Protoplasm is, as we have said, the living part of the body. It is here that metabolism goes on and all the characteristic processes of life take place. The reception of stimuli, conduction, contraction, secretion, reproduction, and so forth take place in the protoplasm alone. The rest of the body exists only to support and protect it. Life is the life of protoplasm.

It is sometimes attempted to recognise in protoplasm a

¹ Chromatin consists of various compounds of the class known as *nucleins*, which contain protein united with another highly complex substance known as nucleic acid, very rich in phosphorus and often in iron. It is probably stored for the use of the nucleus.

truly living part which undergoes relatively little change and a part which is not truly alive, but undergoes the changes which provide the bulk of the life energy, under

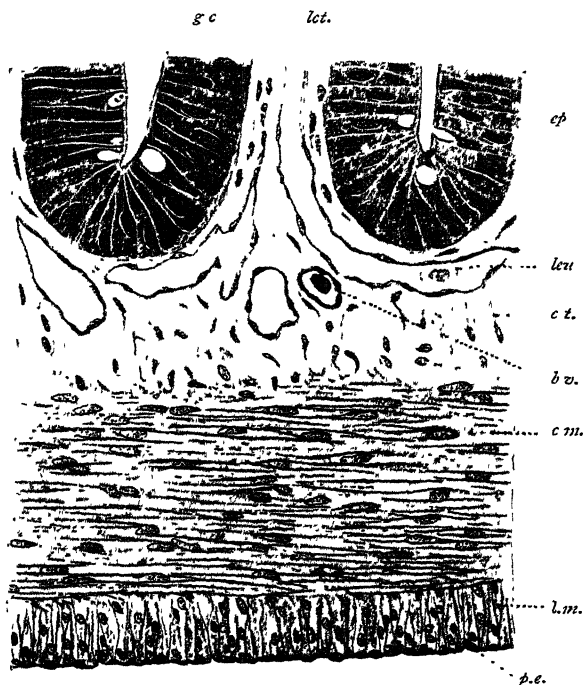


FIG. 46.—A portion of the section shown in Fig. 45, more highly magnified.

b.v., Blood vessel, *c.t.*, connective tissue of mucous membrane, *c.m.*, circular layer of muscle fibres, *ep.*, epithelium, *g.c.*, goblet cell; *l.m.*, longitudinal layer of muscle fibres; *lct.*, "lacteal" or lymph vessel of the intestine; *leu*, leucocyte of lymph or lymph corpuscle; *p.e.*, peritoneal epithelium.

the influence of the living part acting as a kind of ferment. No doubt it is the case that there are many grades of metabolism, but from the broad point of view it is better to regard protoplasm as a single complex mixture of

substances in which there go on the chemical changes which are the basis of the process we know as life.

Every tissue belongs to one of four classes: it is either epithelial, skeletal, muscular, or nervous. The *epithelial tissues* are those which cover surfaces, internal or external. They consist of cells of simple shape arranged to form a layer, with little or no ground-substance between them. When the cells are one layer deep the epithelium is said to be *simple*; when there is more than one layer it is *stratified*. Perhaps the least specialised example of this class of tissue is the kind known as *columnar* epithelium found, for instance, lining the intestine of the frog. This is a simple

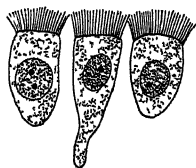


FIG. 47.—Ciliated epithelial cells from the roof of the mouth of a frog.

epithelium, consisting of a single layer of tall cells standing side by side like columns. Between the cells exist exceedingly fine crevices which communicate below with lymph-spaces, and across the crevices the protoplasm of the cells is continuous as fine threads. A modification of this kind of epithelium, known as *ciliated* epithelium, is found on the roof of the mouth of the frog. Here the outer border of the cell is set with very fine protoplasmic hairs known as *cilia*, which are in constant lashing motion in one direction. As they bend sharply and recover slowly, the effect of their combined action is to drive the fluid which covers the epithelium in the direction of their lashing. From each cilium a fine thread runs down into the cytoplasm of the cell. A third modification of columnar epithelium is the kind known as *sensory*. In this some or all of the cells bear at the outer end one or more stiff processes, the size and shape of which varies greatly in different cases. Each such cell is connected with a sensory nerve, either by being itself prolonged internally into a fibre, which runs in the nerve, or by such a fibre ending against it. Cells of this kind are found, for instance, in the olfactory epithelium, where each bears a tuft of stiff bristles, and in the retina, where each ends in a stout rod-shaped or conical body. These compose

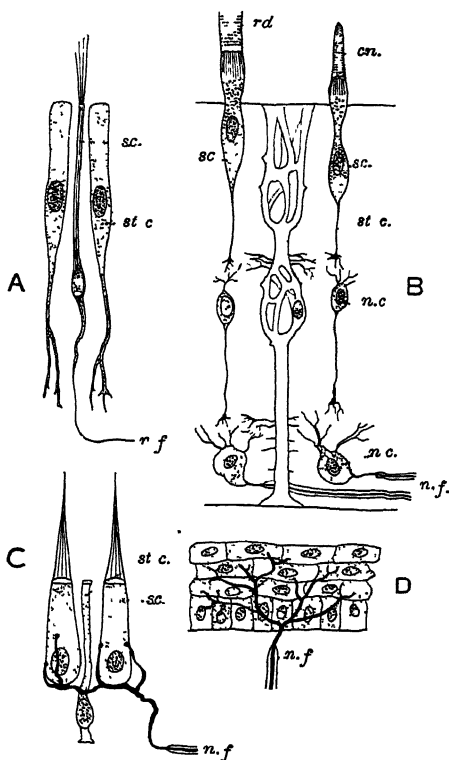


FIG. 48. —Examples of different modes of ending of sensory nerve fibres of the frog.

A, Cells from the olfactory epithelium *B*, cells from the retina. *C*, cells from one of the patches of sensory epithelium in the labyrinth, with which the fibres of the auditory nerve are connected. *D*, a portion of the epidermis, showing the ending of a nerve fibre.

D is ordinary stratified epithelium. *A*, *B*, and *C* are true sensory epithelia—forms of columnar epithelium adapted to the purposes of special senses. In these latter there can be distinguished *sense cells* and *supporting cells*. The sense cells bear processes of various kinds on the surface of the epithelium, and at their other ends come into relation with nerve fibres. In *A* the sense cell is prolonged into a fibre which runs in one of the olfactory nerves as a non-medullated nerve fibre (p. 92). In *B* also the sense cells are prolonged into fibres, though these are connected with the nerve by the intermediation of other cells with whose processes their fibres interlock. In *C*, on the other hand, the sense cells are not continued into fibres, but are embraced by branches of nerve fibres belonging to cells in the ganglion of the auditory nerve. Thus they resemble *D*, where the nerve fibres have a similar relation to the cells of the epithelium. In many of the lower animals, such as the earthworm, the sensory nerve endings in the skin are of the type of *A* and *B*, rather than that of *C* and *D*.

cn., Cone; *n.c.*, nerve cells; *n.f.*, nerve fibres; *rd.*, rod; *sc.*, sense cells; *st c.*, supporting cells.

the layer of "rods and cones" which lines the retina. *Glandular* epithelium is a kind of simple epithelium in which the cells have become specialised for the manufacture or secretion of chemical substances. It may occur as single cells scattered among those of ordinary columnar epithelium. This is seen, for instance, in the intestine of

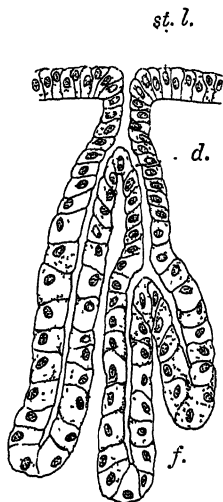


FIG. 49.—One of the glands of the frog's stomach.

d., Duct; *f.*, the secreting part of the gland, known as the fundus or alveolus; *st. l.*, epithelium lining the stomach

the frog, where some of the cells store at their outer ends granules of a substance which, when they discharge it, forms the *mucus* which gives the lining of the alimentary canal and other spaces the name of mucous membrane. After the discharge of this substance there is left a cup-shaped hollow in the cell, on which account it is called a *goblet cell*. The hollow is presently filled again by the activity of the protoplasm of the cell. Isolated gland-cells in an epithelium are sometimes known as *unicellular glands*. Collections of gland-cells form *multicellular glands*. The simplest kind of these is found in the mucous membrane of the stomach. The epithelium here dips down into the underlying connective tissue as hollow tubular processes like the finger of a glove. The mouths of these tubes are lined with ordinary columnar epithelium

which deeper in the tube is succeeded by somewhat lower cells. This region is the *duct* of the gland. At the end of the tube the cells are large and low and contain in their protoplasm granules of a substance which, when it is discharged, forms the enzyme of the juice secreted by the gland.¹ The granules do not leave a hollow in the cell when they are discharged. Such a gland

¹ The granules themselves consist not of the enzyme but of a precursor called the *zymogen*.

is known as a *tubular gland*. The pancreas is an example of the more complicated class known as *racemose glands*, in which the tubes are branched and lined with low, cubical epithelium up to their ends, which are dilated and lined with glandular epithelium. The dilations are known as *acini* and the tubes leading to them as *ducts*.

The liver is more complicated still, the tubes not only branching but joining to form a mesh-work, whose walls consist of gland cells. *Pavement epithelium* belongs (Fig. 5) to the simple class, but is very different from any of those we have seen hitherto. In it the cells are flat, and so thin that their surface is raised where the nucleus lies. They are separated by narrow but distinct lines of *intercellular substance* which stains strongly with silver nitrate, and the surface has then the appearance of being composed of flat

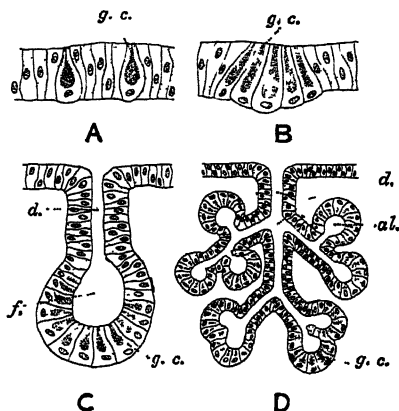


FIG. 50.—Diagrams of different kinds of glands.—Partly after Lang.

- A, Columnar epithelium containing isolated gland cells or *unicellular glands*. B, similar epithelium with the gland cells collected into a group so as to form a *flat multicellular gland*. C, a *hollow multicellular gland* of the simple kind. The figure represents a type intermediate between the *saccular glands* of the frog's skin (Fig. 52) and the *tubular glands* of the frog's stomach (Fig. 49). The latter, however, may be forked, and thus show a transition to D, the *compound or racemose glands*.
al, Alveoli or acini of the racemose gland, d, ducts; f., alveolus or fundus of simple gland; g c, gland cells.

tiles, like a pavement, from which circumstance the name of the tissue is derived. The coelom, blood vessels, and lymphatic vessels are lined with this epithelium. *Stratified epithelium* consists of several layers of cells. It is found in the *epidermis or scarf skin* which covers the surface of the frog's body. In it the lowest layer consists of deep cells with unaltered protoplasmic bodies, but suc-

cessive layers from within outwards become more and more flattened and converted into a horny substance till the outer layer consists of flat, horny scales which are shed, being renewed from within by the division of the lower layer. The inner, softer strata are known as the *Malpighian layer*. *Germinal epithelium* consists of columnar cells with rounded cells derived from them, some of which give rise to ova and spermatozoa. It is found lining the seminiferous tubules of the testes and covering

the surface of the ovaries. The *spermatozoa* are minute structures consisting of an elongated *head*, which contains the nucleus in a very thin investment of cytoplasm, a short *neck*, which consists of protoplasm containing a centrosome (see p. 102), and a *tail*, which has the form of a *flagellum* or lash of protoplasm. The *ova* are large rounded cells containing numerous granules of food

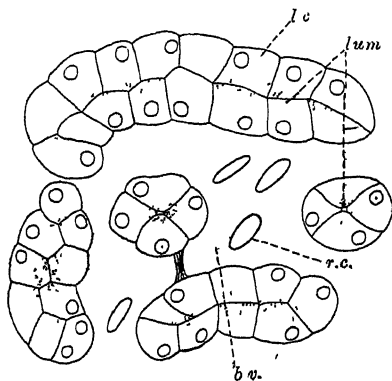


FIG. 51.—A small portion of a section of a frog's liver, highly magnified.

b.v., Blood vessel, l.c., liver cells, lum, lumen of liver tubes; r.c., red corpuscles.

matter or *yolk* and blackened on one side by the presence of *pigment*. On this side lies the nucleus. Each ovum is enclosed in a *vitelline membrane*, and surrounded in the ovary by a case or *follicle* of cells, derived from the germinal epithelium, which manufacture the yolk and pass it to the ovum.

Nervous tissue consists of cells provided with processes for the purpose of conducting impulses. In each such cell or *neuron* there may be distinguished (1) a *cell body*, containing the nucleus, (2) a long process known as the *axon*, along which impulses are discharged, (3) other processes,

usually short, numerous, and highly branched, known as the *dendrites*, along which impulses reach the cell. The

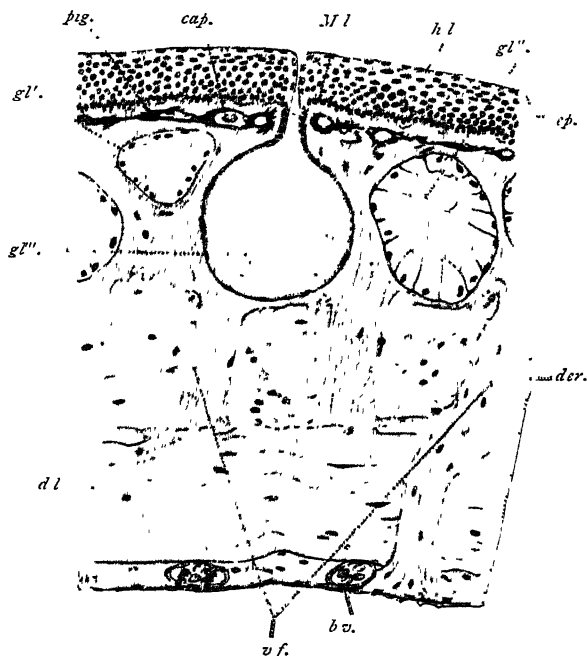


FIG. 52.—A section of the skin of a frog, taken vertically to the surface, highly magnified.

bv., Small blood vessels; *cap.*, capillaries; *dl*, dense layer of connective tissue, consisting of fibres which lie parallel to the surface; *der.*, dermis or corium; *ep.*, epidermis; *gl'*, *gl''*, *gl'''*, glands of three kinds; *gl'* and *gl''* secrete a slimy mucus and pass it to the surface of the skin by ducts which are not shown in the section, *gl'''* secretes a more watery secretion which probably contains a substance of unpleasant taste, all three kinds are simple glands of the saccular type, *hl*, horny layer of the epidermis; *M.L.*, lowest row of the Malpighian layer of the epidermis; *pig.*, pigment cells; *vf.*, strands of vertical fibres in the connective tissue

axon ends by breaking up into a tuft of branches, the *terminal arborisation*, from which a stimulus is given either to another nerve cell or to the elements of some different

tissue, as for instance to one of the fibres which compose muscle. The axon is often of very great length, and is then known as a *nerve fibre*, the term "nerve cell" being applied to its cell body alone. Such a fibre bears at intervals nuclei which, however, do not belong to it, but have a small amount of granular cytoplasm of their own. They are called *nuclei of the sheath*, because they underlie and appear to belong to a delicate membranous *primitive sheath or neurilemma* which generally covers the fibre. Nerve fibres are of two kinds, *medullated* and *non-medullated*. In the former a layer of fatty substance, known as the *medul-*

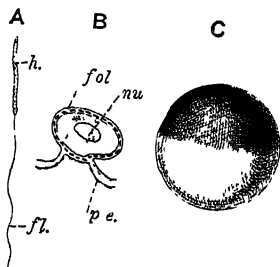


FIG. 53.—Germs of the frog. *A*, spermatozoon; *B*, unripe ovum in the ovary; *C*, ripe ovum. Magnified, but not drawn to scale.

fl., Flagellum; *fol*, follicle; *h.*, head; *nu.*, "germinal vesicle," or nucleus of the ovum, *p.e.*, peritoneal epithelium.

lary sheath, lies between the neurilemma and the axon, which is called the *axis cylinder*. The medullary sheath is broken at intervals at spots known as *nodes of Ranvier*, and the nuclei are arranged one to each internode. In non-medullated fibres the fatty sheath is wanting. Medullated fibres are found principally in the cerebro-spinal system, non-medullated fibres principally in the sympathetic system.

The grey matter of the central nervous system consists of cell bodies embedded

in an exceedingly fine network composed of dendrites and terminal arborisations, with fibres passing through it on their way from the cell bodies. The white matter and the nerves consist of fibres only. Ganglia consist of cell bodies interspersed with fibres, some or all of which make connection with the cells. In the dorsal root ganglia each cell has only one process, and this after running for a short distance divides at right angles, giving off in one direction an axon which enters the central nervous system, and receiving in the other a process which has the structure of a fibre but functions as a dendrite, bringing in impulses from sense cells.

Muscular Tissues. *Muscular tissue* consists of elongated elements, either cells or cœnocytes, known as *fibres*, in which the power of contraction is highly developed. It is of two kinds, *striped or striated*, and *plain*,

unstriped or unstriated. Involuntary muscle (see p. 39) is generally unstriped, voluntary muscle striped. The fibres of plain

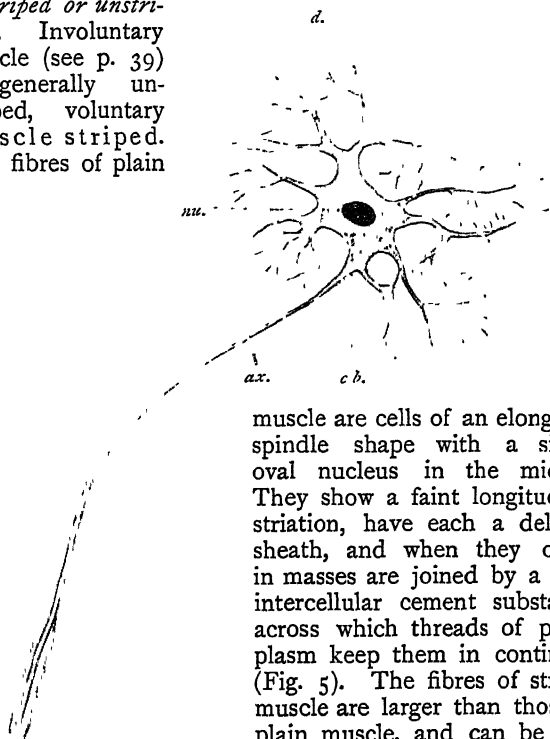


FIG. 54.—Diagram of part of a neuron highly magnified.

ax., Axon; c.b., cell body; d., dendrites; nu., nucleus.

muscle are cells of an elongated spindle shape with a single oval nucleus in the middle. They show a faint longitudinal striation, have each a delicate sheath, and when they occur in masses are joined by a little intercellular cement substance, across which threads of protoplasm keep them in continuity (Fig. 5). The fibres of striped muscle are larger than those of plain muscle, and can be seen with the naked eye if a portion of one of the great voluntary muscles be teased into fragments. Each is a cœnocyte, containing many nuclei. The fibre is cylindrical, tapering at the ends. It is covered by a transparent elastic membrane, the *sarcolemma*, which adheres at the end to that of an adjacent fibre or to tendon. The cytoplasm

is characterised by alternate light and dark stripes which lie across the length of the fibre (Fig. 59). The nuclei are scattered throughout the substance of the fibre, and often each is surrounded by a little granular undifferentiated protoplasm

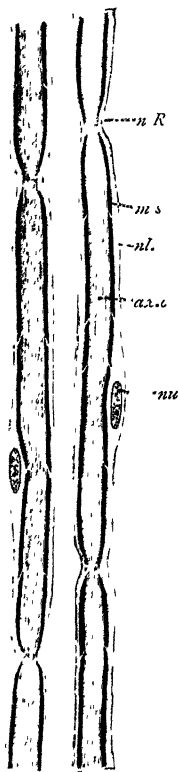


FIG. 55.—Medullated nerve fibres, stained with osmic acid and highly magnified.

ax.c., Axis cylinder; *m.s.*, medullary sheath; *nu.*, neurilemma; *n.R.*, node of Ranvier; *nu.*, nucleus

Note that the axis cylinder contains longitudinal fibrils.

unlike the modified protoplasm which composes most of the fibre. A longitudinal fibrillation is present, but its relation to the striation is a matter of dispute. The muscular tissue of the heart is a peculiar kind of striped muscle known as *cardiac muscle*. It consists of short oblong cells, each with one nucleus, square at the ends, and bearing blunt processes that abut upon similar processes of neighbouring cells. It is striped, but less distinctly so than ordinary muscle. It is in this tissue that the automatism of the heart resides.

Skeletal tissues are characterised

Skeletal Tissues.

by a great development of intercellular or ground substance between the cells, whereby it is adapted to support and bind together other tissues. In *cartilage* the ground substance is a homogeneous *matrix* readily stained by silver nitrate. It is firm and elastic, and sometimes toughened by the development in it of fibres, when it is known as *fibrous cartilage*, in contradistinction to plain or *hyaline cartilage*. The cells are simple in shape and often disposed in groups of two or four formed by the division of one original cell. As these secrete additional ground substance they

become pushed apart by it. In *calcified cartilage* the structure is the same as in hyaline, but the ground substance is impregnated with salts of lime. *Connective tissue*, like cartilage, has a ground substance which stains readily with silver nitrate, but it is much softer and always contains fibres of two kinds—*white fibres*, which have a wavy course, branch but do not join, and are composed of extremely fine fibrils, and *yellow or elastic fibres*, which have a straight course, branch sharply and join to form a meshwork, and are not composed of fibrils. The white fibres swell up and become transparent in acetic acid, the elastic fibres do not. When connective tissue is boiled, the ground substance yields *gelatin*, whereas cartilage treated in the same way gives a substance known as *chondrin*. In the ground substance are a number of irregular spaces occupied by cells or *connective-tissue corpuscles*, of which some are branched and often continuous by their branches, while others are rounded and granular. Connective tissue penetrates every part of the body, holding together the softer tissues and forming in the skin a continuous envelope known as the *dermis*, which is covered by the epithelial epidermis. Tendon is a modified form of connective tissue in which the white fibres are very plentiful and run parallel instead of forming a feltwork. The cells lie in rows between the fibres. *Fatty or adipose tissue* is a form of connective tissue in which the fibres are scanty and most of the cells are swollen into vesicles by the presence of a droplet of fatty matter to which the protoplasm of the cell forms a fine sheath with the nucleus on one side. In the early

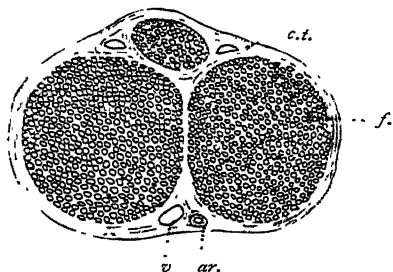


FIG. 56.—A transverse section of a medullated nerve of the frog, stained with osmic acid and magnified.

ar, Artery; *c.t.*, connective-tissue sheath or perineurium; *f.*, funiculus or bundle of nerve fibres; *v*, vein.

others are rounded and granular. Connective tissue penetrates every part of the body, holding together the softer tissues and forming in the skin a continuous envelope known as the *dermis*, which is covered by the epithelial epidermis. Tendon is a modified form of connective tissue in which the white fibres are very plentiful and run parallel instead of forming a feltwork. The cells lie in rows between the fibres. *Fatty or adipose tissue* is a form of connective tissue in which the fibres are scanty and most of the cells are swollen into vesicles by the presence of a droplet of fatty matter to which the protoplasm of the cell forms a fine sheath with the nucleus on one side. In the early

stages of the growth of such a cell small droplets of fat are laid up in the protoplasm, and these grow and run together till they fill nearly the whole cell.

Bone (Fig. 4) has a firm ground substance like cartilage, but differs from it both in composition and in the arrangement of its cells. The ground substance consists of an organic basis impregnated with salts of lime—principally the phosphate. When boiled it yields gelatin. It is arranged in *lamellæ* separated by rows of minute spaces or *lacunæ* which contain the *bone cells* or *corpuscles*. The lacunæ are

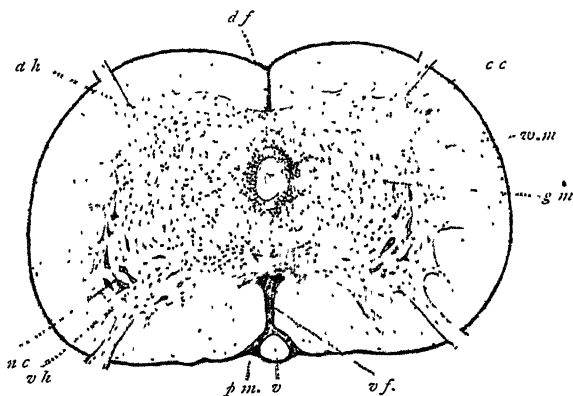


FIG. 57.—A transverse section of the spinal cord of a frog.

c.c., Central canal; *d.f.*, dorsal fissure; *d.h.*, dorsal horn, *g.m.*, grey matter; *n.c.*, large nerve cell, *p.m.*, pia mater, *v.*, vein, *v.f.*, ventral fissure; *v.h.*, ventral horn.

connected by fine *canaliculi*, through which the cells are continuous by minute processes. The lamellæ are arranged in a concentric manner around spaces which contain blood vessels. Some of these spaces are large and filled with a tissue known as *bone marrow*, rich in blood vessels and fat cells. When the layer of bone around the marrow cavities is thick, it is traversed by smaller spaces, known as *Haversian canals*, in which lie minute blood vessels. The lymph from the blood vessels permeates the bone through the canaliculi.

Blood is classed among the skeletal tissues on account of the plentifulness of its fluid ground substance, although

it only acts as a supporting tissue when under high pressure it renders an organ turgid. The fluid part of blood is known as the *plasma*, the cells as *blood corpuscles*. They are of two kinds, *red* and *white*. Each red corpuscle is a flat, biconvex, oval disc, yellow in colour owing to the presence of a compound of a protein with an iron-containing organic substance. This compound is called *hæmoglobin*,



FIG. 58.—A portion of the bladder of a frog, stained and highly magnified.

c.t.c., Connective tissue cell; *m.f.*, unstripped muscle fibres; *n.ep.*, nuclei of the epithelioid cells which cover and line the bladder.

and it has the power of uniting with oxygen to form a loose compound known as *oxyhæmoglobin*, which is formed in the respiratory organs and breaks down in the capillaries of the tissues, yielding its oxygen. Thus it serves as a carrier of oxygen. The same substance is found in the red corpuscles of all backboned animals, but in man and other mammals these corpuscles are round biconcave discs without nuclei. The white corpuscles or *leucocytes* are

colourless and smaller than the red. They have not, like the red, a definite shape, but consist of very soft undifferentiated protoplasm, which has kept its power of contraction, and when the corpuscle lies against a solid surface is constantly changing its shape, putting forth in all directions irregular processes or "pseudopodia" and as readily withdrawing them again. By continually lengthening a pseudopodium and withdrawing those on the opposite side they

can flow along. Movement of this kind is called *amœboid* because it occurs in a minute animal known as *Amœba*, which we shall presently study. In the blood stream the leucocytes take on a rounded shape, so that they are easily bowled along. The white corpuscles are of several kinds. Some of them are of use to the organism by flowing round and thus engulfing into their protoplasm harmful bacteria, which they digest. Such are known as *phagocytes*. At times several phagocytes flow together to form a common mass of cytoplasm containing several nuclei, known as a *macrophage*. Other leucocytes secrete substances which either destroy bacteria or neutralise the poisons that the latter secrete. Leucocytes also carry substances, such as fat globules, from one place to another.



FIG. 59.—A portion of a striped muscle fibre, magnified.

When blood is shed it *clots*, owing to the formation and precipitation in the plasma of a protein known as *fibrin*, in the form of a meshwork of fine fibrils which entangles the corpuscles and forms a firm mass. This is due to the action of an enzyme secreted by the corpuscles. The liquid which remains after the formation of the clot is known as *serum*. The object of clotting is to close wounds and thus prevent loss of blood.

The white corpuscles are semi-independent portions of the organism living in the blood. Each of them retains all the powers of the whole organism. They are irritable, as may be seen by their increased activity on

warming, or by the effect upon them of various drugs. They appear to be automatic, for we can often trace their movements to no stimulus. Their substance must undergo katabolism, for they expend energy, as we have seen, in contraction and in the manufacture and secretion of various substances. The fact that the stimulation of one part of their surface by the presence of a bacterium causes other parts to co operate in swallowing it shows the existence in them of conduction. They assimilate from the plasma nourishing matters to repair their waste. They reproduce by fission, first the nucleus and then the cytoplasm parting into two, and each half of the cytoplasm taking a half of the nucleus. Consisting as it thus does of protoplasm which retains all the primary powers of a living being, the white corpuscle shows us that these powers must be regarded as the birth right of all protoplasm, and that their possession by all organisms is due to this fact, and not to the presence of several kinds of protoplasm. Yet it is important to notice that the independence of the leucocytes is only relative. They are still wholly dependent for their nourishment upon the body by which they were formed, and their activity is directed to the welfare of that body. With the relative independence of the white corpuscles, the condition of the other cells of the body is in contrast. Each of them consists of a portion of the protoplasm of the organism in which certain of its powers are highly

The Differentiation of Cells



FIG 60 —Cartilage stained and magnified, showing cells, some of which are in pairs formed by the division of a single cell, matrix, and the newly secreted part of the matrix, which forms capsules around the cells

sion by all organisms is due to this fact, and not to the presence of several kinds of protoplasm. Yet it is important to notice that the independence of the leucocytes is only relative. They are still wholly dependent for their nourishment upon the body by which they were formed, and their activity is directed to the welfare of that body. With the relative independence of the white corpuscles, the condition of the other cells of the body is in contrast. Each of them consists of a portion of the protoplasm of the organism in which certain of its powers are highly

developed, while others are degraded or lost. It is probable that all protoplasm retains irritability, either to stimuli through a nerve or at least to changes in the composition of the fluid that surrounds it. It may be, too, that automatism of a kind is widespread; and disintegration and assimilation are of course universal. But

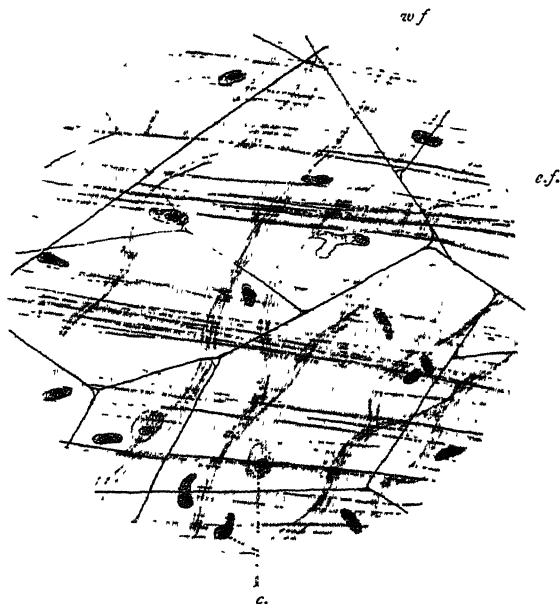


FIG. 61.—Areolar connective tissue of the frog.

c, Cells; *e.f.*, elastic fibres; *w.f.*, white fibres.

in most tissues the cells have lost in the adult the power of reproduction, and certain of the modes of appearance of the energy liberated by disintegration are developed at the expense of others. Thus in a nerve cell conduction is highly developed and contraction lost, while in a muscle fibre conduction is relatively poorly developed and contraction powerful. In both these tissues chemical

manufacture and secretion for the benefit of the rest of the body is at a low ebb, while in gland cells, which are neither contractile nor conducting, it is highly developed. In correspondence with these peculiarities of function go peculiarities of form. That is to say, here as everywhere we find differentiation and the physiological division of labour hand in hand.

The innumerable nuclei of the frog's body have all arisen

Nuclear Division.

by the division of one original nucleus, that of the zygote formed by the conjugation of the ovum and spermatozoon (see p. 9). The process of *nuclear division* by which the nuclei multiply is usually followed by a *cell division* in which each half of the divided nucleus takes its own portion of the cytoplasm which surrounded the parent nucleus, but in some cases, as in the division of the nuclei of a striped muscle fibre, cell division

does not take place, so that a coenocyte arises. Nuclear division is of two kinds. In a few cases, as in some leucocytes, the process is quite simple. The nucleus lengthens, then narrows in the middle so that it becomes dumb-bell shaped, and finally breaks into two at the narrow part. This is *simple or amitotic division*. In most cases, however, a complicated process known as *karyokinesis or mitosis* takes place. The resting nucleus is enclosed by a delicate *nuclear membrane* and appears to consist of a meshwork of a substance known as *linin* with a *nuclear*

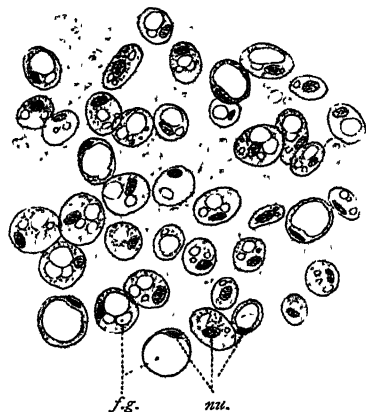


FIG. 62.—Part of one of the fat bodies of a frog, compressed and magnified, showing fat cells with fat globules in various stages.

f.g., Fat globules; nu., nuclei

sap in its interstices. On the theory that protoplasm is an emulsion (see p. 82), the linin is a more viscid liquid which

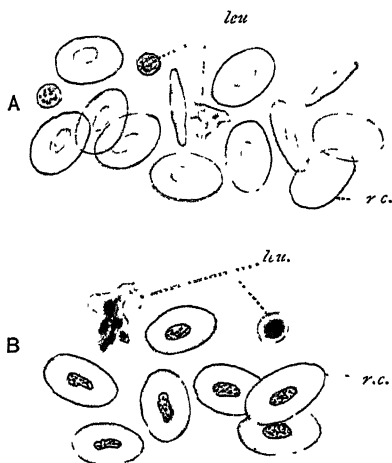


FIG. 63.—Blood of a frog, highly magnified.

A, Fresh, B, stained.

leu., Leucocytes, r.c., red corpuscles.

forms the walls of minute bubbles in which the nuclear sap is held. In the linin lie granules of the deeply-staining substance *chromatin*. There is often also a body known as the *nucleolus*, consisting of a substance which stains differently from chromatin. Outside the nucleus lies a minute body known as the *centrosome*. When mitosis is about to take place, the centrosome divides into two halves which travel to

opposite sides of the nucleus. As they separate, the protoplasm becomes arranged in a radiating manner around each, forming a figure known as the *aster*. Meanwhile the nuclear membrane is breaking up and the nucleus is undergoing certain internal changes. The linin with its contained chromatin granules

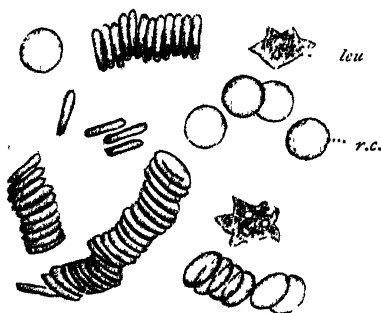


FIG. 64.—Human blood, highly magnified.

leu., Leucocytes; r.c., red corpuscle.

arranges itself into a coiled thread, the *skein or spireme*, which then proceeds to break up into a number of equal portions known as *chromosomes*, of which the same number appears in every nuclear division in the body (but not, as we shall see, in the germ cells). In the frog this number is twenty-four. At this stage there appears, stretching from one centrosome to the other across the site of the nucleus, a structure

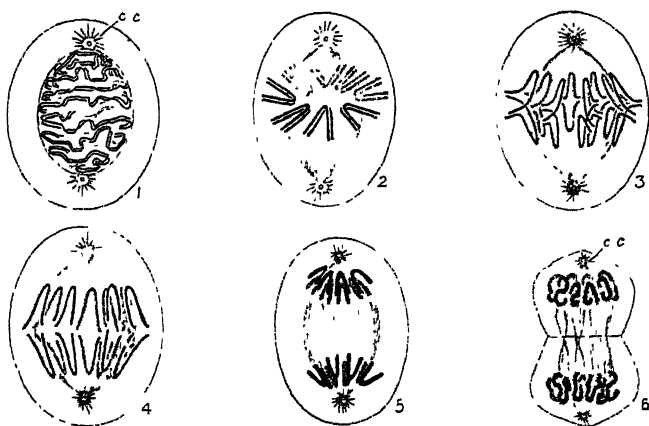


FIG. 65.—Karyokinesis.—After Flemming.

1. Coil stage of nucleus, *cc*, centrosome.
2. Division of skein into U-shaped loops or chromosomes, and longitudinal splitting of these.
- 3, 4. Recessing of chromosomes from the equator of the cell.
5. Nuclear spindle, with chromosomes at each pole, and achromatin threads between.
6. Division of the cell completed.

known as the *spindle*, which consists of fine threads diverging from each centrosome to the equator of a spindle-shaped figure. The chromosomes now become attached to the spindle fibres in a ring round the equator. The next stage consists in the division of each chromosome lengthwise into two equal halves and the passage of the halves or *daughter chromosomes* along the threads towards the poles of the spindle. There they arrange themselves in a radiating manner. Finally, the chromo-

somes of each group thus formed constitute a daughter nucleus by passing through a series of changes which reverse those by which the mother nucleus broke up. They unite end to end to form a skein, and this breaks up into a nuclear meshwork, a nuclear membrane meanwhile forming around it. It will be seen that the result of this process is an exact halving of the linin and chromatin of the mother nucleus between the daughter nuclei. It is often supposed that the object of this process is the inheritance by each daughter nucleus of all the powers of the parent nucleus, but the fact that most of the cells exhibit a part only of the potentialities of the fertilised ovum makes it difficult to accept this interpretation without qualification.¹

The nuclei of the ova and spermatozoa, destined to form **Gametogenesis.** by fusion a single nucleus from which the body nuclei arise, contain each only half the number of chromosomes found in the body nuclei. This is the result of certain peculiarities in the cell divisions by which the gametes arise. The formation of ova and spermatozoa is known as *gametogenesis*. The formation of spermatozoa is known as *spermatogenesis*, that of the ovum as *oogenesis*. Gametogenesis comprises two successive divisions of a cell, derived from the germinal epithelium, known as the *gametocyte*. The gametocytes which give rise to spermatozoa are known as *spermatocytes*; those which give rise to ova are *oocytes*.

The first division of gametogenesis is known as the *meiotic division*. It differs from ordinary mitosis in that by it *the number of chromosomes is halved*. It is therefore called the *reducing division*. The process is complicated by the fact that the true chromosomes come together in pairs before separating, so that the nucleus appears to contain from the first half the number of chromosomes, but these are really double chromosomes. Then each double chromosome parts, so that the daughter nuclei have each half the number of single chromosomes. The *second or post-meiotic division* follows the first without a resting stage. It is a normal division, in which each chromosome splits into two to give rise to one daughter chromosome in each

¹ See footnote on p. 162.

daughter nucleus, so that the daughter nuclei have each half the normal number. At fertilisation the zygote has

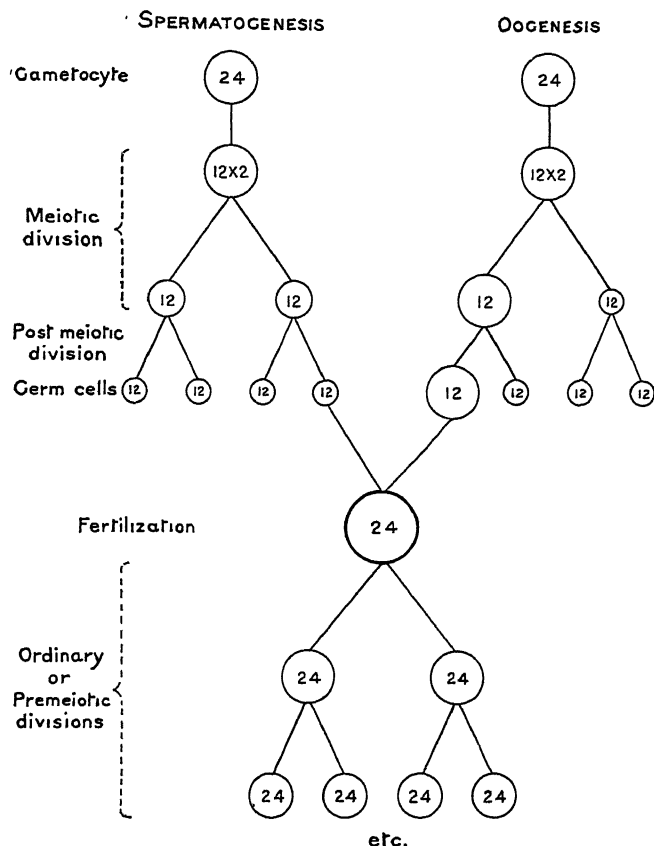


FIG. 66.—A diagram of gametogenesis and fertilisation.

therefore the normal number, which it imparts during mitosis to the body cells.

Thus in the frog gametogenesis follows the course indicated in the diagram above.

The actual course of gametogenesis differs greatly in the two cases. In spermatogenesis the cytoplasm is equally divided and each of the products of division becomes a spermatozoon, so that from each spermatocyte four spermatozoa arise. In oogenesis each division is unequal. At the first division there are formed a large cell and a small one, the latter containing very little cytoplasm and being known as the *first polar body*. At the second division, while the first polar body forms two very small cells,¹ the large cell forms again a large and a small product. The

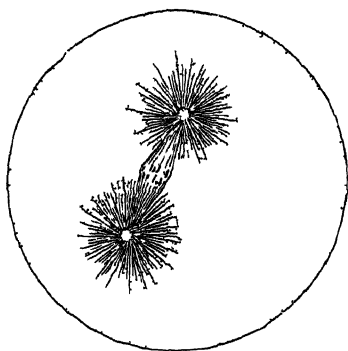


FIG. 67 —Mitosis in the egg of a sea urchin

large product is an ovum, the small is called the *second polar body*. Thus, instead of four ova the oocyte forms one ovum and three vestigial cells which come to nothing. The formation of the polar bodies is known as the *maturaton of the ovum*.

The meaning of these processes is very obscure. It is clear, however (1), that, whatever be the

reason for the occurrence of two divisions in gametogenesis, the fact of these being the same for both kinds of gametes makes the ovum and spermatozoon equivalent bodies, so that they meet on equal terms when they conjugate, (2) that the reduction division is a preparation for conjugation, (3) that in this division the nuclear substance is not evenly divided by the splitting of each chromosome as in ordinary mitosis, but any difference that may exist between the chromosomes will cause the germs to which they are bodily transferred to be unlike.

Only one spermatozoon ever conjugates with any ovum. While the slime around the eggs is swelling up and setting to a jelly in the water, the spermatozoa which have been

¹ In many animals the first polar body does not divide.

shed over it by the male pass through it, swimming by means of their tails. They are far more numerous than the ova and most of them perish, but one succeeds in entering each egg. Its cytoplasm disappears in that of the ovum, but the nucleus passes onward and comes to lie side by side with that of the egg. The two nuclei are known as the *male and female pronuclei*. Meanwhile there has arisen from the neck of the spermatozoon a centrosome, around which is formed an aster. As the nuclei approach one another this divides and forms a spindle. The pronuclei break up each into twelve chromosomes, which lie at the equator of the spindle. Thus the normal number of twenty-four chromosomes is restored, these lie in two groups corresponding to the two pronuclei. Now the chromosomes split in the ordinary way and the halves pass to opposite poles of the spindle, where they form ordinary nuclei. The cytoplasm of the egg meanwhile divides into two cells, known as the first two *blastomeres*. This is the first of the series of divisions known as the *cleavage or segmentation of the ovum*, by which the cells of the embryo are formed (see p. 388).

Sooner or later, to frogs as to men, comes death.

Death However successful the individual may be in avoiding enemies and accidents, he cannot escape that gradual slowing of the working of the bodily machine which in the long run brings it to a standstill. The course of metabolism is in some way limited, so that in the most perfect conditions natural death would eventually result. The nature of this limitation is not understood. The fact that the germs are not subject to it, but produce new individuals with a fresh lease of life, shows that it is not inherent in all protoplasm, but belongs only to that of the cells which constitute the bulk of the body. This it would seem to affect in all tissues alike, so that, were the body not the complicated machine that it is, death might come as a gradual loss of power in all parts alike. As it is, however, the end is always more or less premature as regards some tissues, being brought about by the breaking down of one of the main parts of the machine, as the brain, or lungs, or heart, though in the long-run any other part brings about general death through its effect

upon the heart, whereby the rest of the body is deprived of fresh blood. It may be that this breakdown is due to the protoplasm of the body cells being, as it were, wound up to go for a certain length of time only. It may be that some or all of them produce substances which are slow poisons, and that these in course of time accumulate beyond the power of the body to destroy or excrete them. In any case, so far as our present knowledge goes, death in all the higher animals is inevitable.

CHAPTER VI

AMCEBA

AMCEBA PROTEUS is a little organism found in the mud and on weeds in freshwater ponds. A large specimen is just visible to the naked eye as a minute, irregular, whitish speck. Under the microscope (with transmitted light) this is seen to be a mass of translucent slime, greyish in colour owing to the presence of numerous small, dark granules. The outer layer is clear and transparent owing to the absence of the granules. This layer is called the *ectoplasm*, the granular inner part being the *endoplasm*. In the endoplasm are usually to be seen the remains of other little organisms, especially the brownish plants known as diatoms, which form the food of *Amœba*. At one spot is a round space filled with a clear fluid, which grows gradually larger and then suddenly disappears, owing to a contraction of the protoplasm around it causing it to burst out and discharge its contents into the surrounding water. It then gradually re-forms in the same portion of protoplasm as before. This space is called the *contractile vacuole*. There are usually other small vacuoles which are not contractile. With care there may also be seen in the living specimen a lens-shaped body of moderate size which is somewhat denser than the rest of the protoplasm. This is the nucleus. If the animal be killed and stained with carmine or any of a number of other dyes, the nucleus takes up the stain more deeply than the cytoplasm. The irregular shape of the body is constantly changing, owing to the outgrowth of new processes or *pseudopodia* and the withdrawal of old ones.

The formation of a pseudopodium begins with a slight outflowing of the ectoplasm, into which the endoplasm presently flows. The projection continues to grow by the flow of more protoplasm into it for a varying time, and locomotion is brought about by the persistent lengthening of one pseudopodium till the bulk of the body has been transferred into it. During this time it is throwing out subsidiary pseudopodia in various directions. Before very long, however, the main flow is directed into one of these and the animal

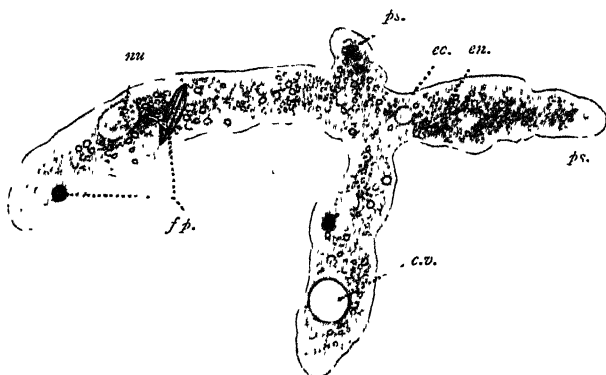


FIG. 68.—*Amoeba proteus*, highly magnified.

c.v., Contractile vacuole, *ec.*, ectoplasm; *en.*, endoplasm; *f.p.*, food particles; *nu.*, nucleus; *ps.*, pseudopodia.

moves in another direction, the stream in the older pseudopodia setting backward into the body until they disappear. The flow of the endoplasm is always swifter in the middle of a pseudopodium than at the sides. It will be seen that we have here an example of *contraction*, as the word is used in Biology, the shape of the mass of protoplasm being changed by the transference of material, but the size remaining the same. The throwing out of a pseudopodium is not brought about merely by a flowing of the protoplasm. The ectoplasm has a certain toughness and its surface is sticky. After the first outflow of ectoplasm has begun to form the pseudopodium, as the endoplasm flows into it, the ecto-

plasm is drawn forward over the back, being lifted up behind the animal and laid down in front. Where it is in contact with the ground its stickiness causes it to adhere. All this can be seen by dropping minute particles of soot on to the back of the animal. They will be seen to stick to the surface, pass forwards till they reach the ground in

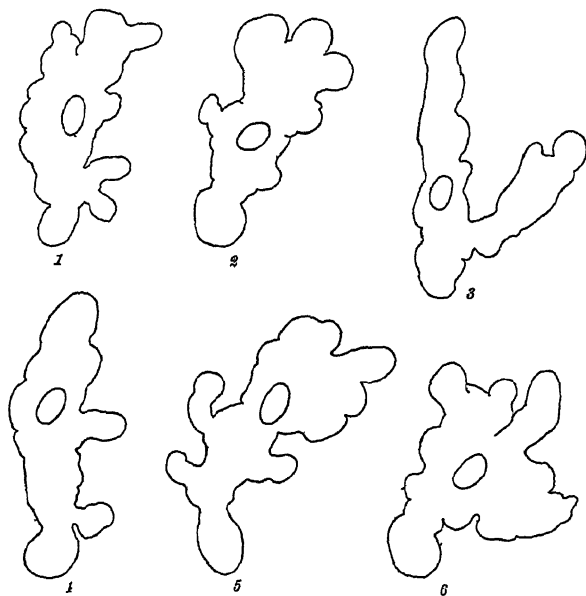


FIG 69 —Successive changes in shape of an individual of *Amaba proteus*, drawn at intervals of two minutes

front of a pseudopodium, and then remain stationary while the animal moves forwards over them, till they come to lie at its hinder end, when they are lifted and carried forwards again over the back. An indiarubber bag filled with water and rolled forward over a flat surface illustrates well the movement of *Amaba*. During the movements the contents of the endoplasm—nucleus, food particles, etc.—are carried about freely from place to place in the body, but the con-

tractile vacuole adheres to the inner surface of the ectoplasm and moves with it. The constant changes of position of internal bodies is one of the arguments which support the foam theory of the structure of protoplasm (see p. 82) against theories which demand the existence in it of a meshwork of fine threads, and an examination under high powers of the microscope confirms this by revealing appearances similar to those found in certain artificially made foams.¹ This is especially noticeable in the outer layer of the ectoplasm, which is a very regular row of minute bubbles known as the *alveolar layer*. The outer walls of

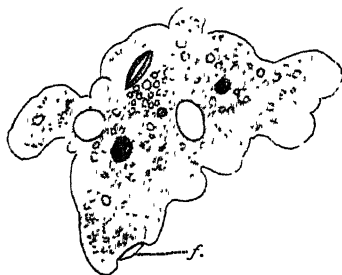


FIG. 70.—*Amoeba proteus* in the act of ingesting *f*, a small vegetable organism which is being swallowed.

these bubbles form a continuous layer which behaves like an exceedingly fine skin. This is known as the *pellicle*, and is believed to be rich in fatty substances. Artificial foams can even be induced to carry out movements which in their general features resemble contraction. It should be noted, however, that the special features of the

contraction of *Amoeba* are not found in them.

Amoeba feeds on small organisms, which it *ingests* by surrounding them with outgrowths of its protoplasm and so engulfing them. Ingestion usually takes place at the hinder end of the animal. The space in the body which the prey comes to fill would thus be lined with ectoplasm, but the ectoplasm here becomes absorbed into the surrounding endoplasm, so that it is clear that there is no essential difference between the materials which compose these layers. There is then secreted around the food particle a layer of water containing substances which kill it and digest its nourishing part.

¹ Such a foam may be made by mixing together rancid oil and salt and placing little droplets of the mixture in water.

The reaction of this fluid is acid at first, but probably later becomes alkaline. The space containing the digestive juice is known as a *food vacuole*. The only organic matter digested by *Amœba* is protein. The dissolved substances are then incorporated and the undigested parts are *egested* by the simple process of being left behind as the animal flows along.

The protoplasm of *Amœba* is irritable, automatic, and conductive. Its *irritability* is shown in various ways. If it be stimulated by passing an electric shock through a drop of water in which it has been placed, it will contract into a mass without pseudopodia. If it be pricked with the end of a fine thread of glass it will draw back and flow away. In this case the formation of a pseudopodium in a region of the body other than that which has been stimulated shows the presence of *conductivity*. Again, the fact that it does not swallow every particle it comes across, but chooses those that contain nourishing substances, shows that it receives from foreign bodies stimuli of different kinds and discriminates between them. In contrast to these instances, many of the actions of the animal cannot be traced to any stimulus, and must therefore be classed as *automatic* in the sense in which we have used that word.

The contractile vacuole is probably an excretory organ. Waste products are shed into its cavity and thus removed from the body when its contents are discharged.¹ Water probably enters all over the surface of the animal and is collected into the contractile vacuole together with the water produced during the katabolism of the animal. The water must bring with it dissolved oxygen, and thus the contractile vacuole aids respiration. At the same time it seems likely that the whole surface of the body may serve to some extent both for respiration and for excretion.

In certain circumstances *Amœba* withdraws its pseudopodia and becomes a rounded mass which secretes about

¹ The nitrogenous waste product uric acid has been found in the contractile vacuole of organisms related to *Amœba*.

itself a tough case or *cyst*.¹ In this it lies dormant and can survive the drying or freezing of the pond in which it lives or be transferred in mud to other ponds. We have here an instance of a widespread phenomena known as *suspended vitality*, and found, for instance, in seeds and in frozen tissues (see p. 84). The exact condition of the protoplasm in such cases is a mystery, but no vital processes can be detected, and it has been shown by experiments on seeds that, if they be kept perfectly dry, not even respiration takes place. We must conclude that life, regarded as a process, has slowed down and, at least in some

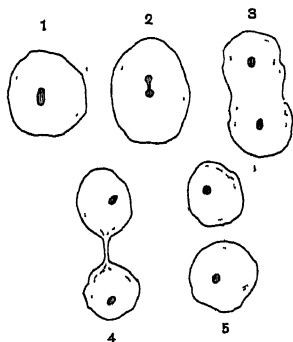


FIG. 71.—A diagram of the fission of *Amaba*. The dark spots represent nuclei.

cases, ceased, but that the protoplasm retains the power of resuming it in certain circumstances. At death, on the other hand, the protoplasm passes into a condition in which it will indeed remain intact in suitable circumstances (as when it is frozen) but has lost the power of resuming life. Many other small fresh-water animals can pass into a state of suspended vitality, and dried mud brought to England from placethousands of miles away will often, on being placed in water, give rise to numerous

creatures that thus lay dormant in it. The artificial suspension of vitality in tissues by freezing has been made use of with very striking results in surgery, portions of living tissue removed from one body being preserved for days in a state of suspended vitality by cold and afterwards successfully grafted in to repair injuries in another body. In this way, for instance, the cornea taken from an eye that had for some other reason been removed from a human patient has been used after several days to replace the

¹ It is doubtful whether the resting cyst of *A. proteus* has been seen. Such cysts are known in other kinds of *Amaba*, and in spore formation (see p. 115) *A. proteus* shows that it has the powers of encystment.

same tissue in another man in which it had been injured.

Amæba reproduces by the process known as **Reproduction.** *binary fission*, in which first the nucleus and then the cytoplasm parts asunder into two halves, each of which appears, at all events, to differ from the parent in nothing but size. In some species of *Amæba* the division of the nucleus is amitotic, but in *Amæba proteus* there is a peculiar kind of mitosis in which the place of centrosomes is taken by a mass of clear protoplasm at each end of the nucleus. These masses are known as *pole plates* and arise within the nuclear membrane, which does not break up during division as in ordinary mitosis.¹ After the division of the nucleus the cytoplasm flows apart into two bodies each of which contains one of the daughter nuclei. The new bodies are at first connected by a bridge of protoplasm, but this becomes narrower until it breaks through and two new individuals come into being. Another kind of fission, known as *multiple fission or spore formation*, has been seen in *Amæba proteus*. During the winter the animal encysted

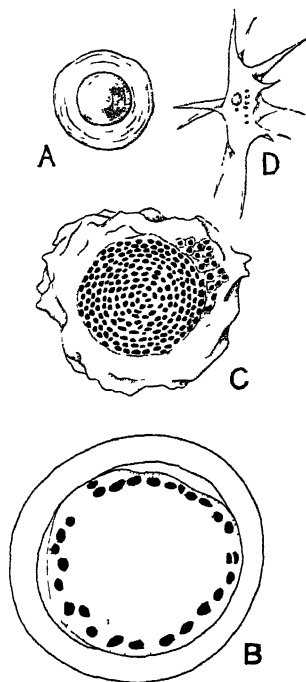


FIG. 72.—Multiple fission of *Amæba proteus*.

A, *Amæba* encysted; B, section of a cyst in which numerous nuclei have been formed; C, surface view of a ripe cyst in which the spores are beginning to separate and the cyst wall to break up; D, a single spore highly magnified.

¹ Not all the chromatin in *Amæba proteus* forms chromosomes. That of the outer part of the nucleus behaves as in amitotic divisions. There is an inner mass which alone takes part in the mitotic process.

and its nucleus divided amitotically till a very large number (some 600) of small nuclei had been formed. These passed to the surface of the cytoplasm, which gathered into a little mass around each of them. The cyst wall was now dissolved and the little individuals or *spores* escaped as small *Amœba* with fine, pointed pseudopodia unlike the blunt processes of the adult, a residual mass of unused cytoplasm being left behind. The young forms grew and became transformed into adults.

Conjugation has not been seen in *Amœba proteus*.¹ The animal does, however, occasionally undergo a process known as *plasmogamy*, in which the cytoplasm of several individuals fuses, forming a single mass which contains several nuclei. Such a mass is known as a *plasmodium*. The macrophages formed by leucocytes (p. 98) are plasmodia. Quite another kind of multinucleate body is found in certain *Amœba*-like animals known as *Pelomyxa*, where two or more nuclei are formed by the division of a single nucleus. These may be compared with coenocytes.²

Our survey of the life and structure of *Amœba* has shown us that it must be regarded as an organism in no way inferior to the frog in its fundamental powers. It is irritable and automatic, undergoes katabolism, contracts, conducts, does chemical work, secretes and excretes, respire, assimilates, and reproduces. It differs from the frog only in the extreme simplicity of its structural organisation, possessing as it does no obvious permanent organs except the cytoplasm, nucleus, and contractile vacuole, and besides these only the temporary organs known as ectoplasm, endoplasm, and pseudopodia. It has no tissues, unless we regard the ectoplasm and endoplasm as tissues unprovided

¹ Supposed instances of conjugation in *A. proteus* have been described, but it has not been shown that the gametes belonged to this species. Conjugation is known in other kinds of *Amœba*.

² They are not coenocytes, which are specialised parts of the protoplasm of the body, whereas *Pelomyxa* is a whole body. Groups of similar, unseparated energids are known as *syncytia*. They may be *plasmodia*, formed by the union of free energids, or *symplasts*, formed by the division of the nucleus of a single energid. A symplast may be a *coenocyte*, or a whole body.

with special nuclei. In many points of structure and behaviour *Amæba* resembles closely the white corpuscles of the frog and more distantly the other cells of the frog's body. It is, in short, a self contained mass of protoplasm with a nucleus—an isolated energid. For this reason it has been usual to regard it as a cell, and to call it a *unicellular organism*, and a theory known as the *cell theory* is widely held, on which the body of such an animal as the frog is said to be a colony of units, each comparable to a single *Amæba*, specialised for co operation with the other cells of the body. But this theory is in reality an inversion of the facts. *Amæba* is a complete and independent organism comparable with the whole body of the frog. Its small size enables all the functions which the nucleoplasm performs to be carried out by a single nucleus. In the frog the size of the body makes necessary a large number of separate nuclei, and the cytoplasm is more or less segregated around these. The energids which are thus isolated as cells have special qualities according to the functions which their position in the body demands. A cell is a portion of the body of a whole organism which has become specialised for the performance of particular functions, not, as the cell theory supposes, a whole organism in which certain functions are suppressed and others highly developed in order that it may co operate with other such organisms to form a body of a higher grade.

The difference between *Amæba* and the frog may be stated in another way. Viewed broadly, the formation of a germ by the frog is a separation of the body

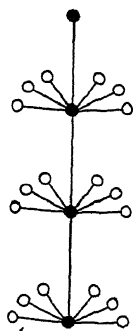


FIG 73 —A diagram of the relation of germ and body substance in the frog. The dark circles represent germs, the light circles body cells. The germ gives rise in each generation to numerous body cells which remain together and eventually die, and also to germs (of which only one is shown in each generation). The germs leave the body and give rise each to a new group of body cells and new germs. Thus the germ substance is immortal, the body substance mortal.

into two portions, one small—the germ—and another large, in which the individuality of the parent is continued. The parent consists mainly of energids which are specialised or differentiated for the performance of certain functions in the body, and are therefore unable to produce energids of other kinds. The germ is an energid which is not thus specialised, and may therefore be said to be “undifferentiated,” though of course it has an organisation of its own. Now the substance of the specialised energids of the parent body is mortal: that is to say, sooner or later it undergoes natural death. But the germ contains substance which is immortal: that is to say, unless it be devoured, or starved, or poisoned, or fail to find a mate, or meet with some other fatality, it will not die a natural death, but in giving rise to a new adult organism gives rise also to another generation of germs, in which it continues to exist within the adult organism until the latter in turn sets free germs. The difference between *Amœba* and animals like it on the one hand, and higher animals like the frog on the other, lies in the fact that in the former there are no body-cells, but the whole body has the immortality of germ-substance.¹ The fission of *Amœba* is a separation of the body into two similar products, neither of which can be said, in virtue either of size or of mortality, to represent the parent. There are two offspring, but the parent has disappeared.

¹ That is not to say that *Amœba* does not contain some substance comparable with the body-substance of the frog, but only that if such substance be present it is not contained in special energids which part from the germs and die.

CHAPTER VII

POLYTOMA

WATER in which organic matter is decaying always contains numerous small organisms of various kinds.

**General
Features.**

Among these, when decomposition is well advanced, there can be found with the aid of the microscope minute, colourless animals of a species known as *Polytoma uvella*, which feed by absorbing from the water through the surface of their bodies substances in solution derived from the decaying matter. The body of a *Polytoma* is an egg-shaped mass of protoplasm without any internal skeleton. A pair of long protoplasmic lashes or *flagella* project from one end; by a backward lashing of these it swims with a definite but somewhat jerky course, the end at which the flagella are placed being forward. The permanent shape of the body is due to a thin *cuticle*, which is not a surface layer of the protoplasm, but a protective covering formed by secretion. It is pierced by two pores for the flagella. Two contractile vacuoles lie close behind the flagella and contract alternately. There is one nucleus, placed somewhat behind the middle, and it is said that there is sometimes a spot of red pigment situated in the front part of the body. The hinder region contains numerous *starch granules*. These must be formed by the protoplasm from substances absorbed in the food: they serve as a reserve of nutriment, and are used up during starvation. Their presence is remarkable, for starch, though it is common in plants, is rare in the protoplasm of animals, which, if they store carbohydrates, usually do so in the form of glycogen. The animals can encyst, and in the encysted state are carried about in dust, etc., to germinate in favourable circumstances elsewhere.

Reproduction is usually brought about by a process known as *repeated fission*, in which binary fission is repeated so as to form four daughters before the young separate, but sometimes there are only two offspring. Fission takes place within the cuticle, this being carried about during the process by the action of the flagella, which remain attached to one of the daughters. The nucleus divides by a kind of mitosis. The first division is transverse and the second longitudinal. When it is completed the flagella are withdrawn, each daughter forms two small flagella, and the cuticle of the parent is dissolved. At intervals of a few days conjugation

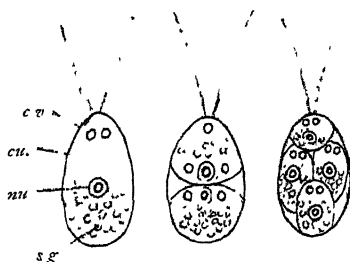


FIG. 74.—*Polytoma uvella* three stages in ordinary fission.

cv, Contractile vacuole; *cu*, cuticle; *nu*, nucleus, *sg*, starch grains

takes place. Two ordinary *Polytomæ* come together and fuse, their nuclei joining and their cytoplasm melting into one mass, which then encysts. After a resting period the zygote divides by repeated fission into eight, each of the daughters grows two flagella, and the cyst is dissolved. In regard to this process we must notice (1) that

since *Polytoma*, like *Amæba*, shows no division into germ-substance and body-substance with special nuclei, conjugation can occur at any time in the life of the individual, and does not need to take place directly after the separation of the germs: in the frog, on the other hand, conjugation is obviously impossible in the adult and can only take place between the little germs, before they develop the rest of the body; (2) that the gametes are alike, and not, as in the frog, of two kinds, a passive kind, which bears the bulk of the cytoplasm, and an active kind, by which is carried out the locomotion which the process involves. Both gametes in *Polytoma* are fairly well supplied with cytoplasm and both are motile. Only when one is older than the other is there sometimes a difference in size. The

conjugation of two like gametes, such as is found in *Polytoma*, is known as *isogamy*: conjugation of unlike gametes is *anisogamy*.

In a later chapter (p. 433) there will be found a description of the flagellate organism *Euglena*, which in various respects resembles *Polytoma*.

CHAPTER VIII

MONOCYSTIS

AMONG the organs of reproduction of an earthworm are certain sacs, known as the vesiculæ seminales, in which the sperm ripens. Here are generally to be found specimens of the parasites known as *Monocystis*, which live by absorbing, through the surface of their body, the fluid in the vesiculæ which is provided for the nourishment of the spermatozoa. Two kinds of these creatures may be present, differing in size and in certain other particulars. The larger kind, *M. magna*, is easily visible to the naked eye as white threads, hanging by one end from the funnels of the vasa deferentia (see p. 188). The smaller, known as *M. agilis*, is more often found free in the fluid among the developing spermatozoa. The body of a full-grown *Monocystis* is long and narrow, and consists of a soft, granular endoplasm and a firm, clear ectoplasm. The endoplasm contains numerous granules, many of which consist of the starch-like substance *paramylum*, and the ectoplasm is covered with a cuticle and has in its deeper layer a network of contractile threads, the *myonemes*. While the cuticle makes it impossible for the protoplasm to flow out into pseudopodia, the myonemes enable it to change its shape by squeezing the fluid endoplasm from one part of the body to another. Slow waves of contraction of this kind are constantly passing along the body. In the endoplasm there is a large nucleus, but there is no contractile vacuole. At one end of the body a small knob or *epimerite* enables it to adhere to one of the cells of the funnel.

In the stage which we have just described, the animals

are known as *trophozoites*. When they are full grown, two of them come together and form them-

Reproduction. selves into a rounded mass without fusing. Around this mass a double cyst is secreted. Each individual now divides by multiple fission, in which the mitosis resembles that of the frog in that the centrosome appears outside the nucleus and the nuclear membrane disappears. There arise thus, as in the spore-formation of *Amæba*, a number of small germs, a certain amount of residual protoplasm being left, which is absorbed by the germs during their development. The germs conjugate in pairs, in which one member is derived from each parent. Thus, although the parents are to all appearance exactly alike, there happens here what happens also in the frog, where the parents are unlike, namely, that the gametes are derived from distinct parents. This is known as *cross-fertilisation*, and is found in the vast majority of cases throughout the animal kingdom, though instances do occur of what is known as *self-fertilisation*, in which gametes derived from the same parent unite.

It is said that in *M. magna* the germs from the two parents are alike, but in *M. agilis* those of one parent—the “female”—are rounded, and those of the other—the “male”—pear-shaped. Each zygote is

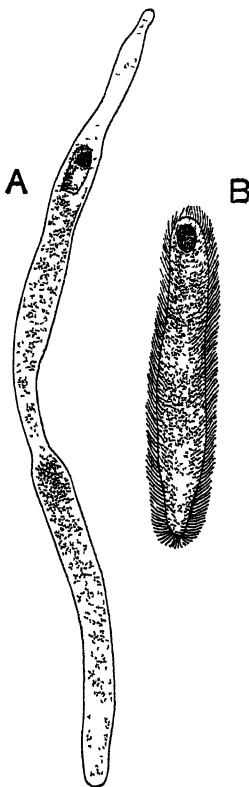


FIG. 75.—*Monocystis*.
A, *M. magna*; B, *M. agilis*. The latter is covered with the tails of spermatozoa, the offspring of the sperm mother cell in which it was embedded.

known as a *sporoblast*; it now secretes a boat-shaped, horny case, and is known as a *pseudonavicella*. Within the case

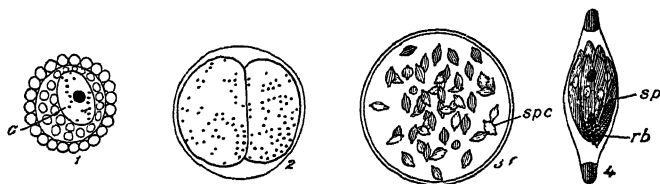


FIG. 76.—The life-history of *Monocystis*.—After Butschli.

1. Young individual (*c*) lying within a sperm-mother-cell of an earthworm.
2. Association of two individuals within a cyst, ready to form gametes.
3. Numerous spore-cases (*sp.c*, pseudonavicellæ) within a cyst.
4. A spore-case with eight spores (*sp*) and a residual core (*rb*).

it divides by repeated fission into eight sickle-shaped *sporozoites*. There are thus two generations of spores¹ in the life history of *Monocystis*. No further development

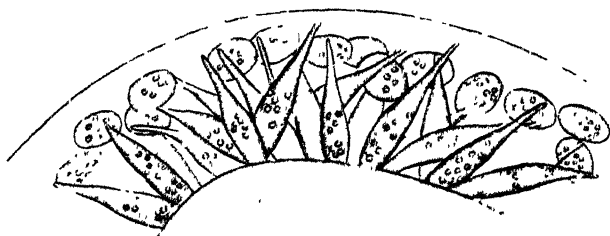


FIG. 77.—Part of a cyst of *Monocystis agilis* showing the two kinds of gametes and the residual protoplasm of one of the parents.—After Hoffmann.

takes place until the pseudonavicellæ get free from the worm, which they generally do by the destruction of the

¹ A spore is a small germ formed by multiple or repeated fission. It may or may not be a gamete. If it be enclosed in a case it is known as a *chlamydospore*, if it is naked as a *gymnospore*.

latter.¹ Probably this takes place by its being eaten by a bird. Protected by their horny cases, the sporozoites pass through the gut of the bird and are distributed in its droppings over the soil, where they are washed down by the rain and presently swallowed by another worm with the earth from which it obtains its food. The sporocyst is dissolved in the intestine of the worm, and the sporozoites come out and bore their way through the wall of the gut and other tissues till they reach the vesiculæ seminales. Here each enters a sperm-mother-cell, where it grows by absorbing the protoplasm which is meant to serve for the nourishment of the spermatozoa (see p. 198). The latter are formed, but wither, their tails only remaining attached to the young *Monocystis*, which looks as though it had a coat of cilia. Finally they disappear, while the *Monocystis* continues to flow. Thus the sporozoites become trophozoites by development.

¹ The details of the transference of the spores of *Monocystis* are very imperfectly known. They *can* pass from one worm to another during coition, but it is believed that this is not the usual method, if indeed it be effective at all.

CHAPTER IX

CILIATA

PARAMECIUM CAUDATUM, the Slipper Animalcule, is a minute animal found in water in which dead

Paramecium: leaves or other remains of organisms are decaying. The decay is brought about by bacteria, and upon these the slipper animalcules feed. A

General Features. rich culture of *Paramecium* may be obtained by steeping hay in water, allowing it to decay, and adding to the *infusion* thus made mud or weeds from a freshwater pond which contains *Paramecium*. The animals may easily be seen with the naked eye as minute, greyish white, oblong creatures, shooting swiftly about in the water. The body of *Paramecium* is spindle-shaped, somewhat flattened on one side, and with one end blunter than the other. The flat side is called "ventral" and the blunt end is anterior. This end appears as though it had been twisted, so that a groove which it bears is spiral, starting in front on the left and curving round to the ventral side, where it is continued back in the middle line to within about a third of the length of the body from its hinder end. The groove is known as the *vestibule* or *peristome*: from its hinder end there passes backwards into the body the funnel-shaped gullet, the opening from vestibule to gullet being known as the mouth. The whole body is covered with fine protoplasmic threads of the kind known as cilia (see p. 86), by whose lashing the animal swims and gathers its food. The cilia are set at equal distances in rows, which run lengthwise in the hinder part of the body, but follow the spiral twist in front: they also line the gullet, where two or three rows of them are fused to form an *undulating membrane* which hangs from the roof. The cilia work regularly in waves, lashing back-

wards and driving the blunt end of the animal forwards, with a rotating movement like that of a rifle bullet owing to its spiral shape.

Like *Amœba*, *Paramecium* is non-cellular. There is a soft, granular endoplasm, and an ectoplasm which is much firmer than that of *Amœba* and gives the body its shape, but is elastic, so that the animal can bend and squeeze through narrow openings. The outermost layer of the ectoplasm is a

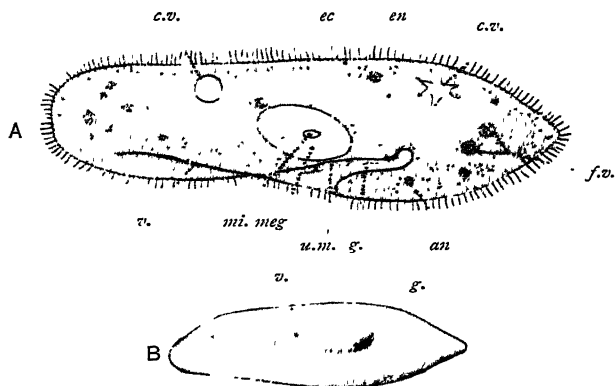


FIG. 78 — *Paramecium caudatum*.

A, An individual seen from the left side, highly magnified; *B*, a diagrammatic view of an individual from the ventral side, less highly magnified.

an, Position of temporary anus; *c v.*, contractile vacuole; *ec*, ectoplasm with trichocysts; *f v*, food vacuoles; *g.*, gullet; *meg.*, meganucleus; *mi.*, micronucleus; *u.m.*, undulating membrane; *v*, vestibule.

thin, tough pellicle. The bubbles of the alveolar layer are indistinct. Under this comes the *cortex*, a thicker, clear layer of ectoplasm in which are embedded peculiar structures known as *trichocysts*. These are spindle-shaped bodies with a sharp point, and consist of some denser substance than the protoplasm. They are placed at right angles to the surface, with the point outwards. If the animal be strongly stimulated, as by a solution of some irritating substance, they suddenly elongate into threads and project from the body. The pointed end is harder than the rest and

remains unaltered as a spear-point. The trichocysts are supposed to be offensive or defensive weapons, but it has never been shown that this is the case. The pellicle is marked by rows of hexagonal pits, in the midst of each of which a cilium arises, while the trichocysts lie under the ridges which separate the pits. Each cilium consists of an axial thread and a covering layer continuous with the pellicle. The axial thread stops short of the tip of the cilium, which is pointed. Below the cilium the thread is continued inwards into the cortex, at the outer limit of which it bears a swelling known as the basal granule. The endoplasm contains numerous granules, some of which appear to consist of waste matters ready for excretion, while others may be stored nutriment. Glycogen is diffused through the endoplasm.

Paramecium caudatum has two nuclei.

These, however, are not both of the same kind, like the nuclei of a *Pelomyxa* (p. 116), but consist of portions of the nucleoplasm specialised for different purposes. One is large and is concerned with the ordinary life of the body. This is known as the *meganucleus*. The other is small and is specialised for the purpose of conjugation. This is the *micronucleus*.¹ We may roughly compare the meganucleus with the nuclei of the body-cells of the frog and the micronucleus with the nuclei of the germs. The nuclei lie in the endoplasm above the gullet, the micronucleus in a cleft in the side of the meganucleus.

¹ The species known as *Paramecium aurelia* has two micronuclei.

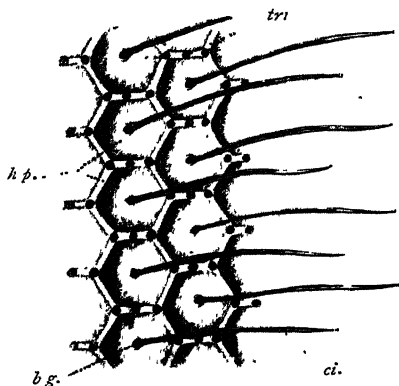


FIG. 79.—A portion of the surface of *Paramecium*, very highly magnified. —Partly after Butschli.

b.g., Basal granule of a cilium; *ci.*, cilium; *h.p.*, hexagonal pits; *tri.*, trichocysts.

There are two *contractile vacuoles*, which lie in the cortex of the dorsal side, one towards each end. At its full size each is a large spherical space surrounded by from six to ten pear-shaped radiating canals, whose wide ends lie under it. These are the *formative vacuoles*. Contraction or "systole" affects only the central vacuole. After it has taken place, the formative vacuoles flow together at their inner ends and thus form the beginning of a new contractile vacuole, round which new canals appear, starting as mere slits and swelling to a pear shape by the enlargement of their inner ends. It is stated that the supposed excretory granules of the endoplasm collect near the formative vacuoles and are gradually dissolved. Over each contractile vacuole there appears to be a soft spot in the pellicle, through which the contents of the vacuole are discharged.

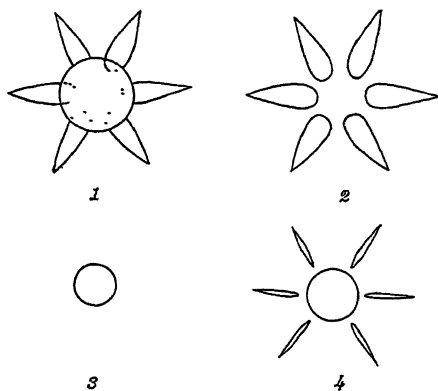


FIG. 80.—Successive stages of the contractile vacuole of *Paramecium*.

The food consists of bacteria and other minute organisms. These are drawn towards the mouth by the current set up by the cilia of the peristome and driven down the gullet by the working of the undulating membrane, which has a waving motion. The pressure of the water driven into the gullet with the food particles causes the naked endoplasm at the bottom of the gullet to bulge inwards, and into the space thus formed the food is forced. A drop of water containing the food particles is now pinched off by a contraction of the endoplasm and becomes a food vacuole, which

is carried by a streaming of the endoplasm around the body, passing first backward along the ventral side, then forward nearly to the middle of the body, then through several turns of a short circuit in this region of the body, and finally forward to the front end and back so as to complete the circuit of the body. During these wanderings the food is digested. The undigested remains are then expelled at a spot just behind the end of the gullet, where a passage through the ectoplasm, known as the *temporary anus*, is formed when it is required. Two periods may be recognised in the digestion. In the first period the water taken in with the food is being absorbed. Substances are secreted into the vacuole during this period which give it an acid reaction and kill the prey. In the second

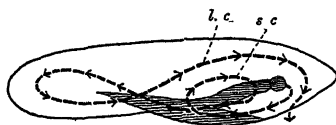


FIG. 81.—A diagram of the course of the circulation of the food vacuoles in *Paramecium*.

l.c., Long circuit; *s.c.*, short circuit.

period an alkaline digestive juice is secreted into the vacuole, which increases in size. It appears that *Paramecium* cannot digest fat.

Like all other organisms, *Paramecium* is automatic.

Effect of Stimuli.

Its incessant activity is spontaneous so far as immediate external stimuli are concerned, but is continually modified by such stimuli. The movements of *Paramecium* are much more active and definite than those of *Amœba*, and it is correspondingly easier to observe the effect of various stimuli upon the animal. These effects are of two kinds, (1) upon the *rate* of movement and (2) upon its *direction*. Many acids, alkalies, salts, and other substances in dilute solutions cause an increase in the rate of motion owing to a more rapid working of the cilia. Moderate increase of temperature has the same effect. On the other hand, dilute solutions of narcotics, such as alcohol, ether, or chloroform, cause the cilia to work more slowly. All these reactions are probably merely the direct effects which such stimuli are known to have upon protoplasm. In order that the effect of stimuli upon the direction of movement may be

observed, it is of course necessary that the stimulus should fall unequally upon different sides of the animal. It will then move to or from the direction in which the stimulus is strongest. This can be arranged by placing with a fine pipette a small drop of some solution in the vessel in which the animals are confined, or by heating or lighting one side only of the vessel. *Paramecium* will move towards weak acids or moderate warmth and away from alkalies, strong acids, warmth above 25°C , etc. Such actions are known as *tropisms*. It was believed that they could be explained in a simple way by the supposition that the effect of the stimulus in each case was either to slow or to quicken the working of the cilia on the side nearest to it, so that the animal was driven mechanically either towards or away from the stimulus by the unequal working of its cilia. What really happens, however, is by no means so simple. The effect of all stimuli to which *Paramecium* reacts naturally is to repel it. The animal on receiving a stimulus first withdraws, by a definite backward movement due to a reversal of the working of its cilia, from the stimulus. It then turns towards the dorsal side and swings the front end of its body round in a circle with that side outwards till it comes to point in some direction in which the stimulus is not acting, and in that direction it swims forwards. Thus its approach to conditions which appear to attract it is in reality due to an avoidance of the relatively less agreeable conditions which it meets in other directions. It behaves as if it were "trying" different directions of movement till one is found from which it is not repelled. It is claimed that in this procedure, known as the *method of trial and error*, the lowest animals, from *Amœba* upwards, show a rudiment of the intelligence of the higher.

Paramecium reproduces by binary transverse fission.

Reproduction The meganucleus divides amitotically, the micronucleus by a mitosis in which, as in that of *Amœba*, the nuclear membrane does not break up, and the place of centrosomes is taken by pole plates. Meanwhile a groove appears round the middle of the body and deepens till the cytoplasm is sundered into two, each half containing a daughter nucleus of each kind and one of

the contractile vacuoles. The two bodies formed by this fission are asexually produced young, analogous to the buds of which we shall speak in a later chapter (p 150). Their development involves not only growth but also the remodelling of the body, since each of them lacks half the outward organs of the parent, while those which it has are too large for it. In a well fed culture, division takes place two or three times a day, but if the animals be ill-nourished it is much less frequent, and if they be starved they cease to divide.

The conjugation of *Paramecium* is a remarkable process, of a kind found only in this creature and in those which nearly resemble it. In it the animal, though in the absence of body cells it resembles *Amœba* and *Polytoma*, forms in a peculiar way gametes which may be compared with those which are thrown off by the cellular body of the frog. The individuals which form the gametes are exactly alike and resemble normal individuals, except that they are somewhat smaller. As a rule, the process begins during the late hours of the night and lasts till the next afternoon. The details are as follows. Two individuals, which we will call *conjugants*,¹ lie side by side with their ventral sides together, the endoplasm becoming continuous in the region of the gullet, which degenerates. We may compare this with coition. The micronucleus of each conjugant leaves its normal position, lies free in the cytoplasm, and grows larger. It then divides twice, and three of its four products degenerate. During these divisions the number of chromosomes is halved, as it is in the gametogenesis of the frog (p 104), though the details of the process differ in the two cases. The remaining micronucleus divides again, this time unequally, the smaller product being the *male pronucleus*, the larger the *female pronucleus*. At this stage we may regard each conjugant as containing two gametes, represented by the two pronuclei. These are analogous to an ovum and a spermatozoon, so that the animal may be said to be hermaphrodite. The true conjugation now takes place. The male pronucleus of each conjugant passes

¹ They are usually known as gametes. This is incorrect. They are not gametes, but parents which form gametes.

over into the other and fuses with the female pronucleus of the latter. The body which belonged to each conjugant comes thus to contain a micronucleus of mixed origin. It is, in fact, a zygote. The zygotes separate and are known as *exconjugants*. Immediately after separation the meganucleus degenerates, splitting up into shreds, which disappear. Thus the meganucleus resembles in the fact of its mortality the body-cells of the frog, though the body as a whole has the immortality of a germ-cell or an *Amæba*. Meanwhile the joint micronucleus of the exconjugant undergoes three successive divisions, so that the body contains eight nuclei. After an interval the body divides into two, each half containing four nuclei, and after a further interval these halves divide, so that there are four individuals, each with two nuclei, one of which becomes a meganucleus and the other a micronucleus.

The conditions under which conjugation takes place in *Paramecium* have been, and are still, the subject of much investigation. Many points still remain to be cleared up, but certain results have now been reached. Conjugation generally occurs at the beginning of a falling off in the supply of food after a period of exceptional plenty that has brought about rapid multiplication. Thus it will often take place in an infusion in which the bacteria, having used up the nourishment provided by the plant remains, are falling off in numbers, and thus the *Paramecia*, after a plentiful

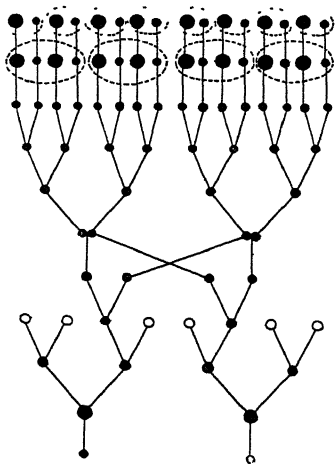


FIG. 82.—A diagram of the behaviour of the micronuclei during the conjugation of *Paramecium caudatum*. The white circles represent the portions which degenerate.

supply of food, are beginning to experience dearth. But there are some races in which it is difficult to bring about conjugation, others in which it has never been seen, and yet others in which it takes place at short intervals without apparent cause. In a later chapter we shall have occasion to discuss the peculiar epidemics of degeneration or "depression" to which *Paramecium* is

liable, and their possible connection with conjugation.

Among the most beautiful

Vorticella: forms of General Features. pond life are the

bell - animalcules, of which the scientific name is *Vorticella*. Various species of these creatures may be found as minute, colourless bodies fastened to weeds by stalks which contract at the slightest disturbance of the water. Some of them also appear in infusions. The

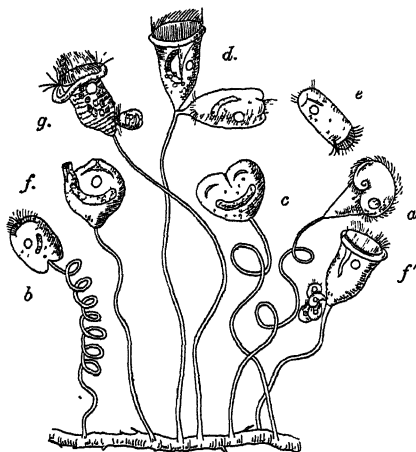


FIG. 83.—A group of individuals of *Vorticella* in various phases of the life-history.

a, Ordinary individual; *b*, the same contracted; *c*, ordinary fission; *d*, a later stage of the same; *e*, free-swimming individual produced by ordinary fission; *f*, *f'*, two modes of fission to form a conjugant; *g*, conjugation.

body of a *Vorticella* is outwardly shaped like a bell, but has no hollow within, the bell being filled with a mass of protoplasm. In the place of the handle is a long stalk, by which the animal is fastened to some solid object. Animals which are thus fixed are said to be *sessile*. The bell can be bent upon the stalk. The wide end of the bell has a thickened *rim*, within which is a groove known as the *peristome*. On one side there passes from the peristome, down into the mass that fills the bell,

a tube known as the gullet. The first part of this is wider than the rest and is sometimes called the vestibule. The part of the upper surface which is encircled by the peristome is known as the *disc*. It is not level, but slopes, being raised on the side where the gullet lies. The disc can be retracted, and the rim of the peristome drawn inward over it. Around the edge of the disc and down into the gullet two rows of cilia wind spirally, the inner row long and standing upright, the outer short and standing outwards. In the gullet the members of the outer row are fused to form an undulating membrane. There are no cilia elsewhere upon the body.

The general character of the ectoplasm and endoplasm is

Ectoplasm and Endoplasm.

the same in *Vorticella* as in *Paramecium*, but the pellicle of the bell-animalcule is sculptured in various ways according to the species, and below it is a distinct alveolar layer. Just

under the alveolar layer, in the walls of its bubbles, is a layer of very fine contractile fibres or *myonemes*. Near the stalk the ectoplasm is much thickened and the myonemes pass inwards through it to join in the middle, where they form a central *contractile fibre* which, with a covering of ectoplasm, makes up the stalk. This is enclosed in a cuticular tube formed by secretion. The contractile fibre is not quite straight, but lies in a

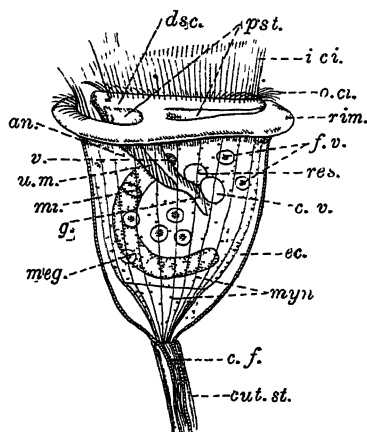


FIG. 84.—*Vorticella*, highly magnified.

an., Position of temporary anus; c.f., contractile filament; c.v., contractile vacuole; cut.st., cuticle of the stalk; dsc., disc; ec., ectoplasm; f.v., food vacuoles; g., gullet; i.ci., inner row of cilia; meg., meganucleus; m., micronucleus; myn., myonemes; o.ci., outer row of cilia; pst., peristome; res., reservoir of contractile vacuole; rim; u.m., undulating membrane; v., vestibule.

very open spiral, so that when it contracts it draws the stalk into a close coil. There are no trichocysts. The endoplasm is granular.

A meganucleus and a micronucleus are present, the former a long, curved band, the latter small and placed beside the meganucleus, usually in the upper part of the body. There is a contractile vacuole, which has no canals. It lies in the upper region of the body and communicates with the vestibule through a *reservoir*, which has a narrow permanent opening. The contractile vacuole contracts sharply at intervals, discharging into the reservoir. The latter then contracts slowly, driving its contents into the vestibule, but not itself disappearing. Feeding and digestion take place much as in *Paramecium*. The little organisms which serve as food are collected and driven into the gullet by the action of the cilia. The food vacuoles follow a definite, winding course in the body, passing through stages similar to those in *Paramecium*. The *feces* are discharged into the vestibule by an anus, which in some species is a permanent opening through the ectoplasm.

The reproduction of *Vorticella* takes place by binary fission, which is of two kinds—ordinary fission, and that which forms conjugants. In ordinary fission, the rim closes in over the disc, the body becomes shorter and wider, and the meganucleus contracts and lies across the body, which then divides into two, the plane of fission being in line with the stalk. The nuclei behave as in *Paramecium*. One of the daughters remains upon the stalk; the other grows a circlet of cilia in the hinder region, at the level at which the ectoplasm thickens, breaks off, and swims away by means of its cilia, to settle down elsewhere by the end which was attached to the stalk of the parent. It grows a new stalk for itself. In this form of reproduction the offspring are equal in bulk. In the fission which forms conjugants the parent gives rise to one large individual and one or more of a smaller size. The small individuals may arise by unequal binary fission, sometimes called budding, or by equal fission, followed by division of one product into four by repeated fission. In either case the small individuals resemble the free product of ordinary fission in all but size.

The small individuals thus formed swim away and each attaches itself by its hinder end to the lower part of the body of one of the stalked individuals. Most of the organs of the small individual now disappear, and the ectoplasm between the two conjugants is absorbed into their endoplasm, which becomes continuous. The meganucleus in each begins to break up and disappear. Meanwhile the micronucleus of the small conjugant has divided into two. Now the micronuclei of both conjugants divide twice, so that the larger contains four and the smaller eight micronuclei. In each case all but one of these perish and the survivor divides into two, which correspond to the male and female pronuclei of *Paramecium*. This division takes place while the two micronuclei are lying in the region where the endoplasm of the conjugants became continuous. One half of each micronucleus passes into the larger conjugant, where the two fuse as male and female pronuclei. The other half of each passes into the smaller conjugant, but these halves, instead of fusing, degenerate and disappear. The endoplasm of the small exconjugant is now drawn into the larger, the ectoplasm shrivelling up and falling off. It will be seen that the conjugation of *Vorticella* takes place in the same way as that of *Paramecium*, but that one of the two exconjugants perishes and is partly absorbed by the other.¹

Carchesium is a small freshwater animal whose body consists of a number of members, each of which has the structure of a whole *Vorticella*. It arises from a *Vorticella*-like body, by divisions like those which take place in the ordinary reproduction of *Vorticella*, save that the division passes some way down the stem and then stops, leaving the bells joined by their stalks. Thus the body is increased by the addition of new members which repeat the structure of the old. In that it increases the number of energids in the body, this process resembles cell formation, but the two cases differ in that the new

¹ The student should beware of comparing the smaller conjugant of *Vorticella* with a spermatozoon and the larger with an ovum. Ova and spermatozoa are gametes of unlike kinds. The conjugants of *Vorticella* are unlike, hermaphrodite parents, each of which forms two unlike gametes.

energids of *Carchesium* all repeat the whole structure of the first and inherit all its powers, whereas a cell is a portion of the body with peculiar characters and restricted powers. The whole body of a *Carchesium* is said to be a *colony*, and its members are *zooids*. Reproduction is brought about by the complete fission from the body of certain zooids, which thus become asexually produced young or buds. When it has broken off and settled down as an independent individual each of these becomes by division a new colony. Conjugation like that of *Vorticella* also takes place.

The detailed study which we have made of *Paramecium*

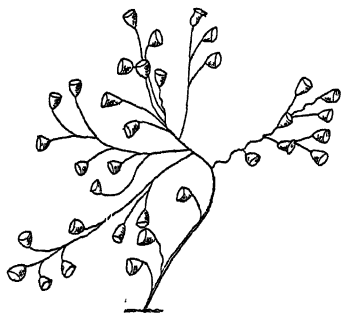


FIG. 85.—A colony of *Carchesium* under low magnification.

Protozoa.

and *Vorticella* has shown to what an extent organisation can be carried without the division of the body into cells. Ranging in grade of organisation between the simplicity of *Amœba* and the complexity of *Carchesium* there is an immense number of animals whose structure is non-cellular. These animals are known as *Protozoa*. Cellular animals are known as

Metazoa. Those Protozoa which move by means of pseudopodia are called *Rhizopoda*, those which move by flagella are *Flagellata*, those which move by cilia are *Ciliata*. Protozoa which, like *Monocystis*, have no external organs of locomotion and form numerous spores are known as *Sporozoa*. In comparing *Amœba* with the frog we noticed that the absence in the former of cells composed of differentiated substance and liable to natural death led to its being, in a certain sense, immortal. The same is true of all Protozoa, although, as we shall see later, the *Ciliata*, in which there is a partial separation of body-substance in the form of a special nucleus, do at times purchase their immortality at the price of the loss of the meganucleus, forming a new one from the micronucleus after conjugation.

CHAPTER X

POLYPS AND MEDUSÆ: HYDRA AND OBELIA

IF a handful of weeds gathered from a freshwater pond be placed in a beaker of water and allowed to stand for a while, there will often be found hanging from the sides of the beaker or from the weeds some short threads of a green, brown, or whitish colour. By one end each thread cleaves to the glass. At the other it bears about half a dozen finer threads, which hang down in the water if they be left undisturbed. A touch will cause these to be withdrawn and take on a shorter and thicker shape, interference with the thread from which they hang is followed by a similar change, and in this way the whole can be made to contract into a vase-shaped mass surmounted by a circlet of little knobs. From time to time water-fleas and other small animals swim against the fine threads and may be seen either to drop through the water as though they were stunned, but afterwards to recover and swim away, or else to remain sticking to the fine threads, which shorten and draw the animal towards the end of the main thread, into which they are swallowed. It is clear that these objects are living beings: in point of fact each of them is a specimen of the animal known as *Hydra*. According to their colour they have been named *H. viridis*, *H. fusca*, and *H. grisea*. The three kinds differ slightly in other respects besides colour, but the following account applies to all of them.

The body of *Hydra* is a hollow cylinder, with a ring of hollow outgrowths or *tentacles* surrounding an opening or mouth at one end, and the other end closed by a flat *basal disc or foot*. The mouth is raised upon an *oral cone or hypostome*; it leads into the hollow of

**Hydra :
General
Features.**

Shape.

the cylinder, with which the hollows of the tentacles are continuous. This space is the *enteron*. The cylinder is rather wider in the middle than at the ends. The wall of the body is composed of two protoplasmic layers, the outer known as the *ectoderm* and the inner as the *endoderm*, with

a *structureless lamella or mesoglea* between them, consisting of a gelatinous substance which they secrete. Such a body as this is known as a *polyp*.

The *ectoderm* consists of several kinds of cells, of which the most conspicuous are those known as *musculo-epithelial cells*. These are roughly conical in shape, with their broad ends directed outwards and fused to form a continuous layer of protoplasm over the body. The apex of the cone is drawn out into one or more *contractile processes*

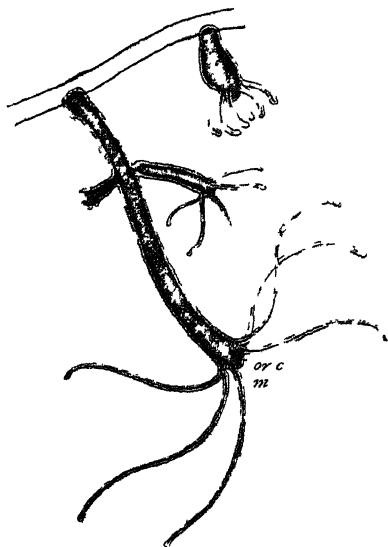


FIG 86 — Two specimens of *Hydra* magnified, one contracted, the other in a state of moderate expansion, the latter bearing two buds in different stages

m Mouth, *or c*, oral cone

which run along the cylinder and tentacles, at right angles to the main part of the cell, forming a distinct layer on the outer side of the structureless lamella. Over the greater part of the body the surface layer of the protoplasm is a firm pellicle, but in the disc this is absent. The cells in this region are also peculiar in containing granules of a substance secreted by the protoplasm which is used to fix the animal to the surface it hangs from. Each musculo-epithelial

cell has a large oval nucleus. In the tentacles these cells are less tall than elsewhere. Between the narrow ends of the musculo-epithelial cells are spaces, which are filled with small, rounded *interstitial cells*. These form a reserve from which, in various circumstances, any of the other cells of the body can arise. Thus they retain the undifferentiated nature of the germs and are sometimes called indifferent cells. Embedded in the continuous layer of the ectoderm are peculiar cells known as *cnidoblasts*. These are very numerous in the tentacles, where they lie in groups or *batteries*, but absent from the basal disc. Each of these has a pear-shaped body with the narrow end at the surface of the animal, where there projects from it a short process known as the *cnidocil*. On this side the cell contains a pear-shaped sac, called the *nematocyst*. The narrow outer end of the sac is tucked in and produced into a long, hollow thread, which lies coiled up in the sac. The space between

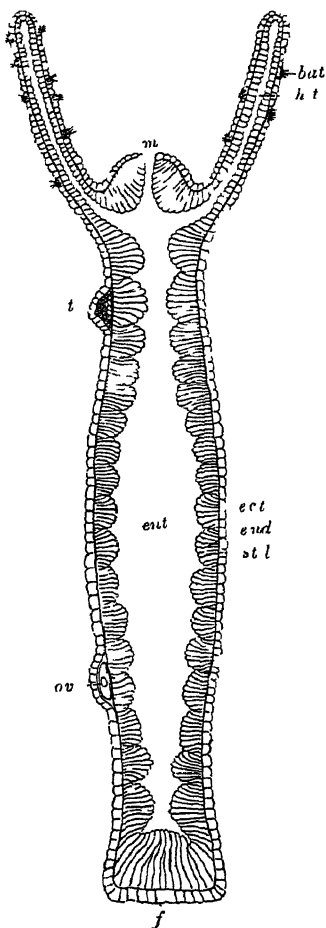


FIG 87 —A diagrammatic, longitudinal section of *Hydra*, magnified —
From Shipley and MacBride

bat, Battery of nematocysts. Only a few of these are shown they cover the tentacles. *ect* ectoderm *end* endoderm *ent* enteron *f* foot *ht*, hollow of a tentacle *ov*, ovary *stl* structureless lamella *t* testis

the thread and the wall of the sac contains a fluid, and there is a specially contractile layer of protoplasm around the sac. The cnidocil is a sense organ. When it is stimulated the contractile layer squeezes the sac and the pressure upon the contained fluid expels the thread, turning it inside out.¹ The nematocysts are of three kinds—a large kind with a straight thread provided with barbs at the base, a small kind with a spiral thread, and a second small kind with a straight thread and a narrower sac than the others. Neither of the small kinds has barbs. The broad end of

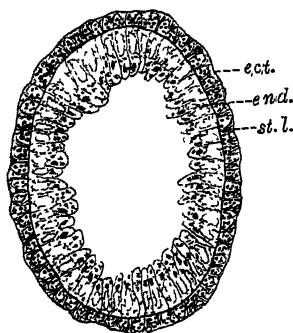


FIG. 88.—A transverse section of *Hydra*, stained and seen under the low power of the microscope.

ect., Ectoderm; *end.*, endoderm; *st.l.*, structureless lamella.

each cnidoblast is anchored into the body by a process which runs inward towards the structureless lamella. The tentacles are covered with a number of warts, each consisting of a large musculo-epithelial cell, in which is embedded a group of cnidoblasts consisting of one or two of the large kind with several of the smaller kinds around them. Each of the kinds of nematocysts has a function of its own. Those of the large, barbed variety are weapons of offence and perhaps also of defence. Their cnidocils are affected by chemical stimuli afforded by the substances given off from

the bodies of other animals. When the nematocysts are discharged, their barbs emerge first and make a wound in the tissues of the prey, into which the thread is driven. In piercing the horny skin of the water-fleas, upon which the *Hydra* principally feeds, they are assisted by the corrosive action of a fluid which they contain, either in the hollow of the tucked-in thread or in that of the sac. This fluid has also a temporary numbing action upon the prey, but the main

¹ It is maintained by some authorities that the thread is expelled not by a contractile layer of protoplasm, but by the swelling up of a jelly which (and not a fluid) they believe it to contain.

purpose of the nematocysts is not to kill but to hold the prey until it is swallowed. In this the spiral nematocysts

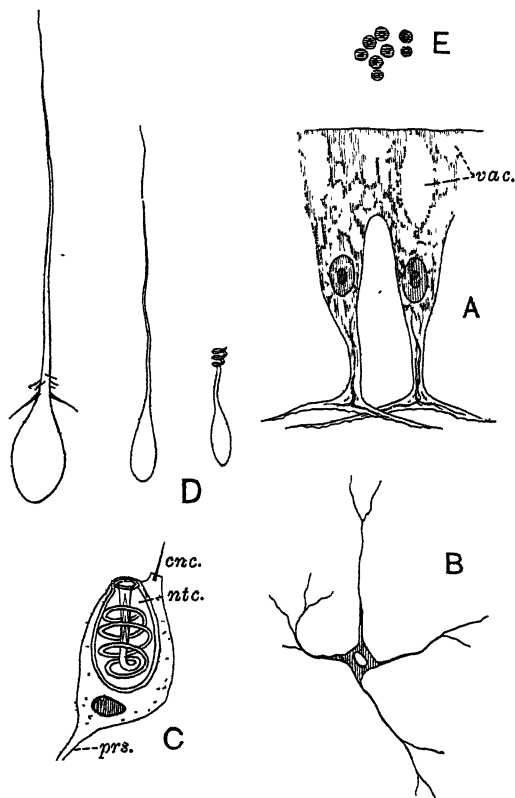


FIG. 89.—The histology of *Hydra*.

A, Two musculo-epithelial cells; *B*, a nerve cell; *C*, a cnidoblast; *D*, nematocysts of three kinds; *E*, Zoochlorellæ.
cnc., Cnidocil; *ntc.*, nematocyst; *prs.*, basal process of the cnidoblast;
vac., vacuoles in musculo-epithelial cells.

assist by coiling round bristles upon the body of the prey. The third kind of nematocysts is of use in attaching the

tentacles of the animal, either to its prey or to other objects when necessary, by the stickiness of their threads. The cnidoblasts arise from the interstitial cells by the formation of a vacuole and its gradual modification into a nematocyst. They are formed in the upper region of the cylinder and migrate thence to various parts of the body, where they take

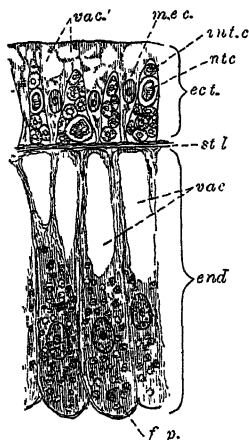


FIG. 90.—A small portion of a transverse section of *Hydra*.

ect., Ectoderm; *end.*, endoderm; *f.p.*, food particle, ingested by an endoderm cell; *int.c.*, interstitial cells; *m.e.c.*, musculo-epithelial cell; *n.t.c.*, nematocyst; *st.l.*, structureless lamella; *vac.*, vacuoles in endoderm cells; *vac'*, vacuoles in ectoderm cells.

up their position in the outer layer. The *germ cells* also arise in the ectoderm from the interstitial cells by a process which we shall describe later. Lastly, the ectoderm contains, in the region where the interstitial cells lie, a meshwork of branching *nerve cells* which are said to be connected with tall, narrow *sense cells* that reach between the musculo-epithelial cells to the surface. Thus *Hydra* possesses a nervous system, but this is in the most rudimentary condition possible, consisting of a continuous sub-epithelial plexus of conducting cells without a central nervous system, while the cell bodies from which the afferent fibres arise are placed among the cells which cover a surface, as in the olfactory epithelium of the frog, not within the body like those of most of the afferent fibres in the latter animal.

In the endoderm the cells are all tall and columnar.

Endoderm.

Certain of them, especially numerous in the oral cone and absent from the tentacles, are *glandular*. They have a narrow stem and a wide end, turned towards the enteron and containing granules of a substance which they secrete. The most numerous and conspicuous cells are *nutritive*. They are columnar, and

have their bases produced into contractile fibres which are shorter than those of the musculo epithelial cells and run around the body, not along it. Their protoplasm contains large vacuoles, and also, in the green *Hydra*, a number of round bodies of a green colour, each of which consists of a central mass of protoplasm with a covering of a different kind of protoplasm containing the green substance known as *chlorophyll* to which the colour of plants is due. These bodies multiply by division. In the brown *Hydra* the green bodies are absent, but there are present some yellowish bodies of similar shape, in which, however, no structure can be made out. It is said that these are also present in the green *Hydra*. The ends of the cells which abut on the enteron bear flagella, which can be withdrawn and replaced by pseudopodia.

The green bodies of *Hydra viridis* have been shown to be individuals of a minute plant known as *Zoochlorella*, which have simple and degenerate structure. Like other plants, they nourish themselves in a manner radically different from that of animals. This they do by means of the chlorophyll. Absorbing certain rays of light, that substance enables the protoplasm, in some way not yet understood, to use the energy of such rays in breaking up molecules of carbon dioxide taken in from the surroundings, which in the case of land plants is the air, in water plants is the water, and in the green bodies of *Hydra* is the protoplasm of the animal. The carbon thus obtained is combined with the hydrogen and oxygen of water also absorbed, to form sugar¹. The oxygen of the carbon dioxide is set free. This can easily be shown in the case of water plants, from whose leaves in sunlight a stream of fine bubbles of oxygen may be seen to ascend. It has been shown that oxygen is also given off from the body of the green *Hydra*. The sugar is used on the one hand for the manufacture of the carbohydrates, in which the plant body is usually very rich, and on the other hand for the formation of the various substances which the protoplasm of plants, like that of animals, requires for food, and in particular of proteins. The nitrogen, sulphur, and phosphorus for this purpose are obtained by most plants as salts in solution in the water.

¹ The substance first formed is Formaldehyde, H COH

they take in, by their roots or sometimes by the whole surface of the body. The green bodies of *Hydra* obtain these elements in certain waste products of the metabolism of the animal which they absorb. It may be that the *Hydra* absorbs from them in return the excess of carbohydrates which they form; and this would account for the absence from them of starch, which is so constantly found in plants. Thus there is between the two organisms a partnership, in which the animal benefits by the removal of waste products and the supply of oxygen and possibly of carbohydrates, and the plant benefits by the rich supply of nitrogenous material and carbon dioxide. Such a partnership is known as *symbiosis* and is in strong contrast with parasitism, in which one of the partners benefits at the expense of the other. *Hydra*, *Zoochlorella*, and *Polytoma* are examples of the three kinds of nutrition found among living beings. While the food of animals, which consists of complex organic substances, is usually in the state of a solid or of the viscous liquid of protoplasm, and has to be swallowed through an opening, the materials taken in by green plants are simple inorganic substances which can be absorbed as gases or liquids through the surface of the body. Plants which have no chlorophyll, such as fungi, and some animals which live as parasites or in decaying matter, absorb their nourishment through the surface of the body, but take it in the form of organic substances, more or less complex in various cases, derived from the bodies of other organisms. Thus there can be distinguished three kinds of nutrition: (1) *holozoic*, in which the food is organic and is swallowed; (2) *holophytic*, in which the food is inorganic and is absorbed through the outer surface; (3) *saprophytic*, in which the food is organic and is absorbed.¹ It must, however, be understood clearly that these differences concern only the form and manner in which food enters the body. The food which is incorporated by the protoplasm always contains complex organic substances.

¹ The modes of nutrition classed under the general title "saprophytic" vary greatly in detail, ranging from cases in which the food is not greatly more complicated than that of a plant, save that sugar is substituted for carbon dioxide, to cases which differ from holozoic nutrition only in the way in which the food enters the body.

The movements of *Hydra* are carried out mainly by the muscular processes of the cells, though the surface of the basal disc can put forth pseudopodia, and it is possible that by means of these the animal can slowly change its position. The muscular processes of the ectoderm cells, when they contract, make the body shorter and wider ; those of the endoderm make it narrower and longer. The position of rest is one of moderate extension. *Hydra* does not remain passive in the absence of stimuli, but, after standing for some time extended in readiness for prey, it automatically contracts either the whole body or the tentacles only, and then extends in a new direction. Thus it explores the whole of its surroundings. From time to time it changes its position. This is done by extending the body and bending it, so that the tentacles touch some neighbouring object and adhere to it by means of the nematocysts with sticky threads. The basal disc is then either withdrawn altogether from the spot to which it was fixed and put down in a new spot close to the tentacles, or caused to glide up to the tentacles. In either case the effect of the process is that the animal moves in somewhat the same way as a looper caterpillar. A *Hydra* responds to every stimulus, except that of food, by contraction. If the stimulus be weak it affects only the part of the body to which it is applied, as a single tentacle will withdraw from a slight touch ; if it be strong its effect spreads to the whole body. A stimulus applied to one side of the body a number of times causes it presently to move away in some other direction.

The food of *Hydra* consists of water-fleas and other small animals. These are caught by the tentacles, and carried by them to the mouth, which then opens and swallows the prey. The animal will not feed unless it be hungry. If it be well fed, creatures which swim against the tentacles are allowed to escape, but if food has been scarce as soon as the prey has become temporarily attached by the nematocysts to one tentacle the others bend over towards it and help to secure it and push it towards the mouth. If the animal be starving the mere smell of food in the neighbourhood is enough to set the tentacles working, but usually

Movements and Reactions.

Nutrition and Excretion.

they are not put into action till the food has been both smelt and touched. It is not possible to deceive the *Hydra* into swallowing substances, such as pieces of blotting-paper, which do not smell like food, but blotting-paper soaked in beef tea is swallowed when it touches the tentacles. Once swallowed, the food is passed deep into the enteron and there softened by a juice which the endoderm secretes and broken up by the churning which it gets as the body expands and contracts. Part of the food is dissolved in the enteron and absorbed in solution, part of it is taken up by pseudopodia of the endoderm cells and digested within their protoplasm. Presumably the ectoderm is nourished by substances passed on from the endoderm, either by diffusion through the structureless lamella or along the fine threads of protoplasm which put the two layers into connection across it. The undigested remains of the food are driven out of the mouth by a sudden contraction of the wall of the body. After a long period of high feeding the animals become liable to depression much like that of *Paramecium*, in which the powers of movement, feeding, and fission are affected and death ensues. *Respiration* and *excretion* probably take place from the surface of the ectoderm and endoderm; there is no special organ for either process.

The species of *Hydra* reproduce themselves both sexually and asexually. The sexual reproduction of *H. viridis* and *H. grisea* takes place normally in the spring and summer, that of *H. fusca* in the autumn. The animals are usually hermaphrodite, but strains are met with in which the sexes are separate. The generative organs are ectodermal structures developed when sexual reproduction is about to take place. The ovaries, of which there is generally only one in each individual, are found in the lower part of the body; the testes, of which there are several, are in the upper part. In the early stages of both organs the interstitial cells multiply and push out the musculo-epithelial cells so as to form a swelling. In the case of the ovary one of the interstitial cells becomes an oocyte. This increases in size and begins to throw out pseudopodia, by which it swallows the rest of the interstitial cells contained in the swelling. At the same time it lays up

in its protoplasm numerous dark, spherical granules of yolk. As the swelling increases, the musculo-epithelial cells are stretched, their conical bodies forming long stalks, which are pushed apart by the oocyte, and their outer layer forming a thin covering for the latter. When the oocyte has swallowed all the surrounding cells it withdraws its pseudopodia and becomes a large rounded body, about which a gelatinous coat is secreted. Polar bodies are now formed, the covering of musculo-epithelial cells parts and shrinks back so that the ovum is exposed save for the gelatinous coat, and fertilisation is effected by one of the spermatozoa which are present in the surrounding water. In the formation of a testis the multiplication of the interstitial cells stretches the musculo-epithelial cells as in the ovary. The interstitial cells become spermatocytes, which lie among the stalks of the musculo-epithelial cells and undergo two divisions as in the frog, the resulting cells developing into spermatozoa with a conical head, a neck, and a tail. By the breaking of the covering layer the spermatozoa are set free and swim in the water, where they perish unless they find a ripe ovum. Since either the ovary or the testis generally ripens first, cross-fertilisation will usually take place, but it does not appear that self-fertilisation is impossible.

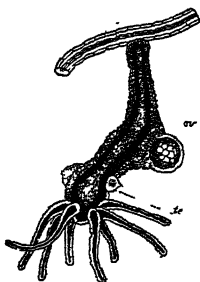


FIG. 91.—*Hydra* hanging from water-weed.
—After Greene.
ov., Ovary; te., testes.

After fertilisation the oosperm undergoes cleavage into blastomeres (p. 107), which as they increase in numbers form at first a hollow sphere known as the *blastula*, whose wall consists of a single layer of cells. Some of these migrate into the hollow, which they fill. The outer layer now represents ectoderm and the inner mass endoderm. The cells of the ectoderm become smaller than those of the endoderm and lose their yolk granules. A thick, prickly covering of a horny substance is now secreted by the ectoderm, and the round, prickly body thus formed falls away from the parent and rests for several weeks, during which it may be carried about by currents, in mud, etc. After a time the ectoderm differentiates into musculo-epithelial and interstitial cells, the jelly is secreted, the shell cracks, and the embryo projects. A split in the endoderm forms the enteron, tentacles grow out, a mouth is formed, and finally the young *Hydra* frees itself

from the remains of the shell, moves away, and begins to feed and grow.

Asexual reproduction also begins with the formation of a swelling of ectoderm by the multiplication of the interstitial cells, which afterwards become converted into musculo-epithelial and endoderm cells, passing through the structureless lamella for the latter purpose. The result of this is an

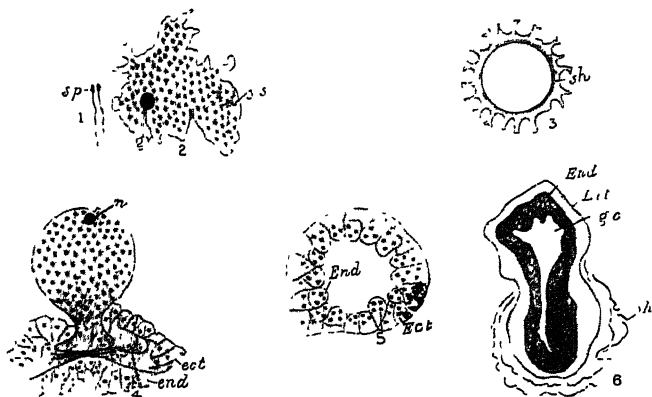


FIG. 92.—The development of *Hydra*.—After Brauer.

1. *sp*, Spermatozoa.
2. Amoeboid ovum; *g.v.*, germinal vesicle or nucleus, *ys*, yolk spherules.
3. Ovum with lobed envelope (*sh*.) around it.
4. Ovum protruding; *n*., the nucleus; *ect*, the ruptured ectoderm; *end*., the endoderm.
5. Section of blastosphere—*Ect.*, ectoderm; *End*., endoderm—being formed.
6. Section of larva. *Ect.*, ectoderm; *End*., endoderm, *g.c.*, enteron, *sh*., ruptured envelopes.

increase in the extent of the ectoderm and endoderm which leads to a bulging of the body-wall. The knob or *bud* thus formed becomes longer, tentacles grow out around its free end, a mouth is formed, and finally the base narrows till the bud breaks free as a new individual, which grows till it reaches the size of the parent. The buds arise in the middle of the body of the parent. Several may be formed at the same time, and a bud may form secondary buds before it is set free. While it is still on the parent, the bud is wholly a

part of the body of the latter. Each of the layers of the parent is continuous with the corresponding layer of the bud, a suitable stimulus is transmitted by the nervous system from one to the other, and the entera are in free communication, so that food obtained by either is available for the other. Occasionally a *Hydra* will reproduce by fission into two, either lengthwise or transversely, of the whole body. In this case, as in the fission of a *Paramecium*, the structural development as well as the growth of each product of fission takes place after separation, whereas in the bud, as we have seen, the structural development takes place before fission.

A property akin to asexual reproduction is that of **Regeneration.** *regeneration* or the replacement of lost parts, which is possessed by *Hydra* in a very high degree. To some extent all organisms have this power, but as a rule the higher the animal the less is its faculty for regeneration. In Man it is little more than the power of healing wounds. Not only will *Hydra* grow anew any part, such as a tentacle, which is cut off, but any fragment of the body, provided it be not too small and contain portions of both layers, will grow into an entire animal.

We must now look at the budding of *Hydra* from a somewhat different point of view. By the out-
Hydroid Colonies. growth of buds, the animal increases the size of its body in precisely the same way as *Carchesium*; that is to say by the addition of new members, each of which repeats the whole structure of the body as it existed at first. In the case of *Hydra* the process is carried further by the fission of the repeated part from the parent body, so that an act of reproduction takes place, but it is easy to imagine a case in which this would not happen. The result would be the permanent conversion of the body of the *Hydra* into a colony, of which the buds would be the zooids. Now there are a number of animals related to *Hydra* in which this actually takes place. Such animals are known as *hydroids*, and nearly all of them are marine. A common example is *Obelia geniculata*, which is found growing upon seaweeds near low watermark on the British coast.

Certain comparatively unimportant differences distinguish the polyps of *Obelia* from those of *Hydra*. The tentacles are more numerous and, instead of being hollow, have a solid core of large endoderm cells, with very stout walls of inter-cellular substance and highly vacuolated contents. In the ectoderm the muscular fibres are independent cells with nuclei of their own, lying below the epithelium. The hypostome is very large and forms a chamber above the rest of the enteron. From the middle of the basal disc of each polyp the body-wall is continued as a narrow tube, which joins the tubes from other polyps so as to form a branching structure like the body of a flowering plant. This is continuous at its base with a root-like arrangement of tubes on the surface of the seaweed, known as the *hydro-rhiza*. The tubes of the whole structure are known as the *cænosarc* and the polyp heads as *hydranths*. The whole colony is enclosed in a horny case or *perisarc*, which is secreted by the ectoderm and follows closely the outline of the body, but is separated from it by a small space, bridged by processes from some of the ectoderm cells. At the base of each hydranth the perisarc expands into a cup or *hydrotheca*, into which the hydranth can be withdrawn.

Obelia:
Anatomy of
the Polyp.

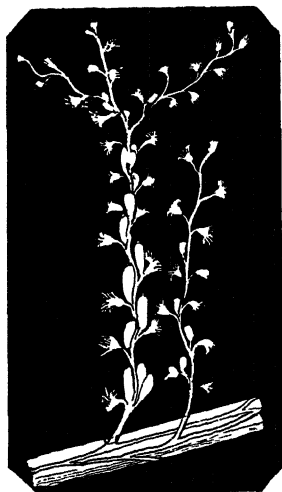


FIG. 93.—Part of a colony of *Obelia*, seen under a hand lens.

The generative organs are not borne by the polyps, but by special bodies, which originate as members of the colony, are set free by breaking away as the buds of *Hydra* are, and carry out sexual reproduction as independent individuals. These individuals differ

The Medusa.

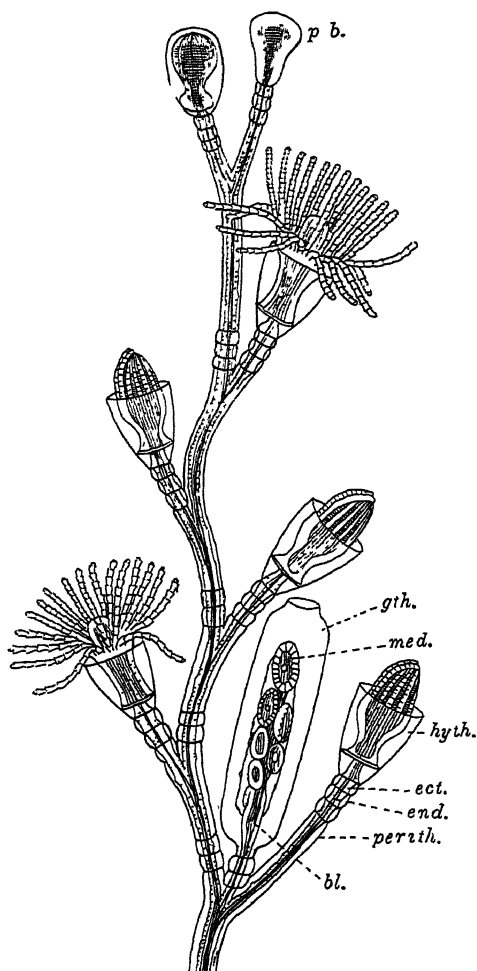


FIG. 94.—Part of a colony of *Obelia*, magnified.

bl., Blastostyle; *ect.*, ectoderm; *end.*, endoderm; *gth.*, genotheca; *hyth.*, hydrotheca; *med.*, medusa bud, *p.b.*, polyp bud; *perith.*, peritheca.

widely from the polyps, being, indeed, so unlike them that their origin from the colony would never have been guessed unless it had been seen to take place. They are small *jellyfish or medusæ*. Each has the shape of an umbrella with a short, thick handle and a fringe of tentacles around the edge. The convex upper side is called the *exumbrella*, the concave lower side the *subumbrella*, the handle

the *manubrium*. Around the edge of the umbrella a low ridge projects inwards. This is the *velum* and represents a much larger structure in the same region of many other medusæ. At the end of the manubrium is the mouth, which leads by a tubular gullet along the manubrium to a stomach in the middle of the body. From this four *radial canals* run outwards to a *ring canal* at the edge of the umbrella. The lining of all these internal

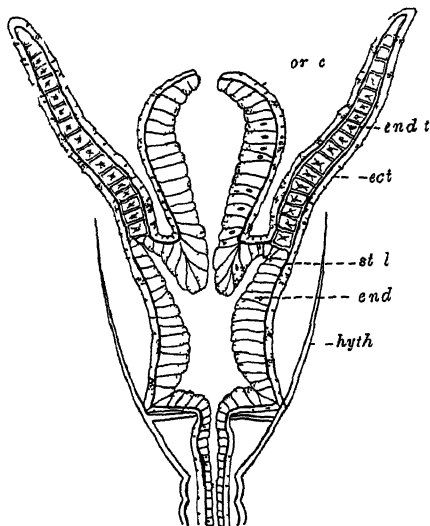


FIG 95 —A longitudinal section of a hydranth of *Obelia*, highly magnified

ect, Ectoderm *end*, endoderm *end t*, endoderm of the tentacles *hyth* hydrotheca *or c* oral cone *st l* structureless lamella

spaces consists of endoderm, and the radial canals lie in a sheet of endoderm, known as the *endoderm lamella*. In fact we may regard the internal cavities of a medusa as corresponding to the enteron of a polyp in which the walls have come together over a large area, leaving certain spaces which form the gullet, stomach, and canals. The whole outside of the body and tentacles is covered with ectoderm. Between the ectoderm and the endoderm is a

layer of jelly which is very thick, especially on the exumbrella side. The medusa may be compared to a polyp which is greatly widened and shortened, the walls of the wide,

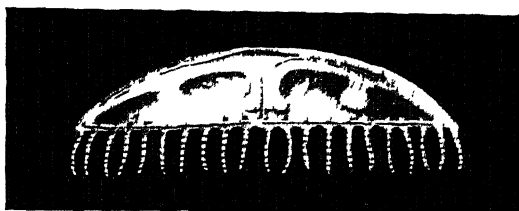


FIG 96 — A medusa of *Obelia*, magnified

flat enteron coming together in places, as we have seen, and the structureless lamella increasing in thickness to form the jelly. The manubrium represents the oral cone and the tentacles stand around it at a greater distance owing to

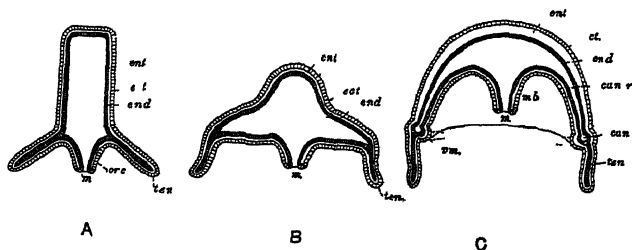


FIG 97 — A diagram to illustrate the relation between polyp and medusa

A, The polyp *B* an imaginary intermediate form *C*, the medusa

can c, Circular canal *can r*, radial canal, *ect*, ectoderm *end*, endoderm *ent*, enteron *m*, mouth *mb*, manubrium *or c*, oral cone *ten* tentacle *zm*, velum. The dotted line represents the velum as it is found in many medusæ but not in *Obelia*.

the widening of the body. The arrangement of the organs of a medusa is an excellent example of what is known as *radial symmetry*. In bilateral symmetry (p 23) the parts of the body are arranged on each side (right and left) of a

plane in such a way that no other plane will divide the body into two halves which are alike. In radial symmetry the parts of the body are arranged about a point in such a way that innumerable planes divide the body into like halves.

The medusa floats in the sea with the manubrium downwards and the tentacles hanging like the snaky locks of its classical namesake. It swims by contractions of the plentiful musculature of the subumbrella side, which drive water out of the umbrella and send the animal forwards in the opposite direction.

Movements of the Medusa.

These movements are co-ordinated by the *nerve rings*—two specially well-developed circular tracts of the nerve plexus situated at the edge of the umbrella. We have here the rudiment of a central nervous system, and it is interesting to find that the animal is paralysed if the nerve rings be cut away. Balance is kept by means of eight sense organs, known as *statocysts*, situated each at the base of one of the tentacles. These are small hollow vesicles containing calcareous bodies and lined

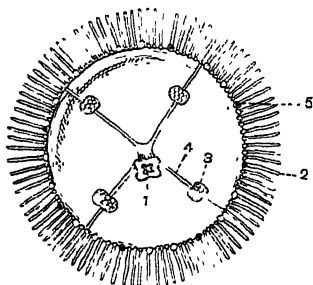


FIG. 98.—The medusa of *Obelia*, seen from the subumbrella side.
—From Shipley and MacBride.

1, Mouth, at end of manubrium; 2, tentacle; 3, gonad; 4, radial canal; 5, statocyst.

by cells from which fine sense hairs project into the vesicle. The swaying of the calcareous bodies give rise to impulses by which the movements of the animal are directed through the nerve ring.

The medusæ are of opposite sexes. The generative organs are not developed till after the animal is set free. They are four in number and lie on the subumbrella below the radial canals. Each consists of a knob of ectoderm, into which passes a short branch from the radial canal. The germ-mother-cells originate in the ectoderm of the manubrium, migrate into the endoderm, and pass along the radial canals to the generative

Reproduction.

organs, where they migrate into the ectoderm again. When the ova or sperm are ripe, they are shed by the rupture of the ectoderm into the water, where fertilisation takes place. As in *Hydra*, segmentation leads to the formation of a hollow blastula. From this, by immigration of cells at one spot, there is reached a stage with a solid mass of endoderm such as that found in *Hydra*. The animal at this stage is egg-shaped and has a ciliated ectoderm, by which it swims freely for a while. It is known as a *planula*.

An enteron is formed by a split in the endoderm, and the planula then settles down by its broader end, forms tentacles and amouth at the other end, and develops into a polyp, from which by budding a colony arises. When the colony has reached a certain size there appear, in the angles between the stem and the branches which bear the hydranths, tubular outgrowths known

as *blastostyles*, each enclosed in a vase of perisarc known as a *gonotheca*. A blastostyle and its gonotheca are together known as a *gonangium*. The blastostyle is probably an incomplete zooid. On its sides are formed a number of buds which develop into little medusæ and escape through the opening at the top of the gonotheca.

It will be seen that *Obelia*, like *Hydra*, reproduces itself both sexually and asexually. Sexual reproduction is carried out by the medusa and leads to the formation of polyps. The asexual reproduction consists in the budding off of medusæ from the polyp

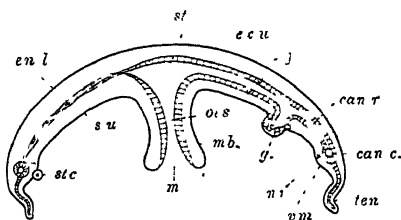


FIG. 99.—A diagram of a vertical section of the medusa of *Obelia*. The section is supposed to pass on one side along a radial canal, and on the other across the endoderm lamella. In reality this would not be possible, since the canals are opposite one another.

can. c., Circular canal; can. r., radial canal; en l., endoderm lamella; ex u., exumbrella surface; g., gonad; j., jelly; m., mouth; mb., manubrium; n r., nerve ring; œs., oesophagus; s. u., subumbrella surface; st., stomach; stc., statocyst; ten., tentacle; vm., velum.

Alternation of Generations.

stock. Whereas, however, in *Hydra* the two processes go on side by side, sometimes in the same individual, and succeed one another quite irregularly, in *Obelia* there are two different types of individual—the polyp stock and the medusa—which follow one another regularly and are each confined to one method of reproduction. Thus we have a definite *alternation of generations*, a sexual and an asexual form succeeding one another. It will be remembered that a similar alternation of generations occurs in *Monocystis*. The asexual generation of *Obelia* is relatively inactive, gathering much nourishment and spending little: the sexual generation is active, spending its substance freely in locomotion, which ensures the distribution of the species, and thus opening up fresh food supplies and increasing the chances of escape from enemies. Here, as in sexual reproduction, we find a distribution of labour among individuals.

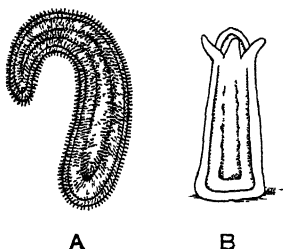


FIG. 100.—A, Planula larva; B, the young polyp into which the planula grows after settling.

The above explanation of the reproduction of hydroids differs in one respect from that which

is generally given. It is usual

to regard the formation of a colony by budding as a kind of asexual reproduction in which there are formed numerous "individuals" which do not separate. In that case the alternation of generations contains an indefinite number of acts of asexual reproduction between each two sexual acts. We have preferred to treat the polyp stock as one individual, containing a number of semi-independent parts—the hydranths—each of which repeats the structure of the whole body as it was at first, together with certain other parts—the blastostyles and most of the coenosarc—which arise in the course of development to serve the entire body and are wholly dependent upon it. The relation between development and reproduction which this view involves may be stated as follows. Any part of an

organism, from the smallest organ to the whole body, is liable to be repeated, with or without differences between the repeated parts. This phenomenon has been called *merism* we have seen it in cilia, trichocysts, contractile vacuoles, cells, limbs, zooids, etc. Sometimes, as in cilia, cells, or zooids of the same kind, it has not involved differences. Sometimes, as in cells or limbs or zooids of different kinds, it has involved differences between the repeated parts. Sometimes the parts are present in their full number from the first, sometimes they increase in number as growth goes on. From time to time every organism produces a part which not only repeats its whole structure, but also separates from it by an act of fission. This process is reproduction. In some cases of reproduction, as in the budding of *Hydra*, the repetition of structure takes place *before* separation. In other cases, as in the formation of germs,¹ the part which separates is simple in structure, but has the power of repeating the structure of the parent body *after* fission. It will be seen that merism is one of the results of the process which we have called development. Working on the large scale development produces from the reproductive body a body like that of the parent, working on a smaller scale it produces from portions of the body substance structures which are like other structures within the body. It is also at work in regeneration.

We have seen that the term *individual* is often applied to the several hydranths of *Obelia*. This term has been used in zoology with very different meanings. (1) As has been said, it is applied to the several zooids of a colony. (2) On the other hand, it is applied to "all those animal forms taken together which proceed from a single egg." This use of the term is simple enough in the case of animals like the frog whose every act of reproduction is sexual, so that only one separate being exists between each ovum and its successor, but in the case of animals which have asexual reproduction it involves the position that numerous separate beings constitute a single individual. Thus in *Obelia* the polyp stock and all its

¹ In this case there may be the additional complication that two such separated parts so develop as to produce but one body after fusion.

medusæ are separated parts of one individual, and in Protozoa all the thousands of beings that may be formed by fission of one zygote constitute a single individual.

(3) We shall not use the term in either of these senses, but shall take it in its simplest significance, regarding as an individual the whole of any organism so long as it is continuous and leads an independent existence. In this sense the act which makes an individual is the act of fission by which it becomes independent of its parent, and fertilisation is the blending of two undeveloped individuals into one, while the polyp stock is an individual which consists of a number of units meristically repeated, and the medusa is an individual consisting of one such unit.

Merism is shown in the formation of new zooids both in *Hydra* and in *Obelia*. In *Hydra* all the zooids separate and all are alike. In *Obelia* only some of the zooids separate, and these—the medusæ—repeat the original structure of the body with great modification. In *Hydra* the life-cycle by which the structure of an individual is reproduced involves a single act of fission. In *Obelia* it involves two.

CHAPTER XI

REPRODUCTION AND SEX

IN the various animals which we have so far studied, we have come across a number of examples of reproduction, occurring in various ways and in different circumstances. It will be well at this stage to consider the process from a broad point of view. We have seen that the essence of every act of reproduction is the origin, by fission from the body of an animal, of a reproductive body, and the development of the latter into the likeness of its parent, and that a process of reproduction is said to be asexual or sexual according as the reproductive body does or does not undergo the process known as conjugation before it develops. Reproductive bodies which differ thus in their behaviour have a corresponding difference in their constitution. This appears clearly on comparing the two kinds of reproduction as they occur in *Hydra*. Asexual reproduction is relatively a simple matter. It consists in the formation of a reproductive body known as a *bud* and its fission from the body and development, although in *Hydra* the structural part of the development is completed before fission takes place.¹ In the bud there are from the first both differentiated energids—the ectoderm and endoderm cells derived from the parent body—and energids which are undifferentiated in the sense in which we have used this word in considering the germs of the frog (p. 118),² for the

¹ Except in the case of longitudinal and transverse fission.

² We may repeat that the word “undifferentiated” as applied to a germ means that it is not as a whole specialised for the performance of any function within an organism, and has therefore the power of giving rise to energids of all the kinds found in the body. It does not mean that portions of the protoplasm of a germ—as for instance

bud contains cells which will later give rise to germs. Thus the body divides into two parts, but these are alike in composition, each containing both germ-substance and body-substance. Sexual reproduction is a more complicated process. It involves the formation of reproductive bodies which shall conjugate before they develop. Since conjugation can only take place between single energids, each reproductive body in sexual reproduction must be a single energid, and since it is to reproduce the whole organism, it must not be specialised for any function within the body. Thus in the formation of the reproductive bodies of sexual reproduction there is a separation of undifferentiated energids from the rest of the body. A reproductive body which consists of a single undifferentiated energid,¹ is known as a *germ*. Ova and spermatozoa are germs. Usually, but not always, germs must conjugate before they can develop. When they do not conjugate, they have the characters of ova, and the process of reproduction is called *parthenogenesis*. This occurs in various insects, crustaceans, and worms. Thus in the rose fly (*Aphis*) the female reproduces for several generations without the assistance of males, and in certain kinds of water-fleas and the minute water animals known as rotifers fertilisation has never been seen.

With the reproductive processes of *Hydra* it is not difficult to compare those of the Ciliata. These animals, though they are not divided into cells, possess, as we have seen, a body nucleus or meganucleus, and a germ nucleus

the tail of a spermatozoon—are not specialised. It does, however, involve the view that some part of the substance of the germ is not specialised in the way that the substance of the body energids is specialised, but is capable of giving rise to such substance. What this part may be does not certainly appear, though it is often asserted to reside in the nucleus alone. The “immortality” of germs and Protozoa appears to accompany it. It is not necessary to suppose that the difference between the body energids and the germs is brought about by the formation of the former from only some of various kinds of substance possessed by the latter. It may well be due to the presence of some factor which allows only some of the potentialities inherited from the germ to come to fruition. In this case the apparently equal distribution of the germ nucleus during the mitoses of development could be reconciled with the loss of potentialities in the body energids.

¹ Possibly in the male gamete of the ciliata of a nucleus only.

or micronucleus. The ordinary fission is asexual reproduction, each nucleus contributing to both offspring. The processes which are known as the conjugation of the Ciliata constitute an act of sexual reproduction, consisting in the formation of germs, their union, and a process of development of the zygote. The difference between the germ formation of the Ciliata and that of the Metazoa is due to the absence of body-cells in the former. The body nucleus is destroyed within the parent body, so that the latter becomes a germ as well as the separated portion. Thus there arise two germs, of which one has little if any cytoplasm and is a male gamete, while the other, which keeps most if not all of the cytoplasm of the parent, is a female gamete. In *Monocystis*, also, both sexual and asexual reproduction are found. The trophozoites give rise to a number of germs which conjugate to form the sporoblasts. The latter give rise asexually to the sporozoites, and these, when they have grown into trophozoites, reproduce sexually again. There is not within the body of a *Monocystis* any such obvious freeing of germ- from body-substance as is found in Metazoa and Ciliata, but it may be that in the discarding of the residual protoplasm some such separation occurs. In *Polytoma* and *Amæba* all the fissions are acts of asexual reproduction. It may well be that the bodies of these animals contain matter which is comparable to the body-substance of the Metazoa, but there is in any case no separation of body- and germ-substance, and in each act of fission the protoplasm is evenly divided. In *Polytoma* conjugation occurs between ordinary individuals, and is not part of an act of reproduction. In *Amæba proteus* it is not at present known to take place.

We have now seen, in a survey of the reproductive processes of a number of animals, that they present a series, in some members of which, as in *Amæba* and certain strains of *Paramecium*, sexual reproduction is not known to occur, while in others it alternates more or less regularly with asexual reproduction, and in yet others, as in the frog, it replaces the latter entirely. This replacement may be explained by the sup-

**Reproduction
of the
Protozoa.**

**The Meaning
of Sexual
Reproduction.**

position that, while in a relatively simple animal asexual reproduction is a less complicated process than sexual, and therefore involves less expenditure of energy, in the formation of a very complex body this advantage disappears, and, because sexual reproduction must for some reason occur from time to time, it comes in the latter case to be the sole mode of increase of the species. We are led to inquire what may be the reason of the occurrence of sexual reproduction. In considering this we must note (*a*) that sexual reproduction involves conjugation, (*b*) that in order to bring this about it has to effect a parting of the undifferentiated or germ-substance from differentiated substance if these exist separately in the body, (*c*) that these two processes are not inseparably bound up together. On the one hand in parthenogenesis we get an isolation of germ-substance without conjugation, and on the other hand in *Polytoma*, where the body of ordinary individuals answers the requirements of a gamete, and perhaps also in *Monocystis*, conjugation is unaccompanied by any separation of germ-substance from body-substance. The isolation of the germ-substance need not be considered further. Its occurrence from time to time appears to be a necessity of life in animals which have distinct body nuclei, and in these animals it is effected either in the course of sexual reproduction or by parthenogenesis, but to regard it as the primary object of sexual reproduction would be to leave unexplained the occurrence of conjugation during that process. We have already shown why the isolation of germs necessarily forms part of most acts of sexual reproduction (p. 162).

There remains the question of the meaning of conjugation. This process always consists in the fusion of two energids known as gametes, whose nuclei and cytoplasm so unite that there results a single energid called a zygote. Gametes are generally germs, but in some Protozoa, as in *Polytoma*, they are adult bodies. In examining the meaning of conjugation we shall be justified, by the elaborate preparations which are often made for it, in assuming that it is in some way beneficial, and not merely brought about by certain circumstances without regard to

**The Meaning
of Conjugation.**

the welfare of the being in which it occurs. The problem is to discover what is the benefit which it confers upon the organism. With regard to this several theories have been held.

(1) On account of the fact that the conjugation of the germs of higher animals is followed by the rapid nuclear division which leads to the cell formation of development, it has been supposed that the process is primarily a *stimulus to nuclear division*, which is needed in certain cases. But if that were so the nuclear division which leads to fission in *Paramecium* ought also to be quickened by conjugation, whereas we find here that conjugation takes place *after* a period of frequent divisions and is followed by a *slackening* in the rate of division—unless, indeed, a new period of plenty ensue, in which case it is the food supply, not conjugation, which is responsible for the quickening of fission. Conjugation must meet some need other than the stimulation of division. Since, however, in the higher animals the whole body cannot conjugate, their germs consist each of a single energid and are thus able to undergo this process. The germs are, moreover, incapable of passing out of their simple condition by development until they have first conjugated, and it may be that this is a precaution against their missing conjugation and thus losing its benefits, whatever these may be. Thus conjugation imparts to them a stimulus to division, but this stimulus is not inherent in conjugation; it is added to it in certain cases. Parthenogenetic ova do not need the stimulus of conjugation, and in the unfertilised eggs of various animals—conspicuously, for instance, in those of sea-urchins—it has been found possible, by the use of certain solutions of salts and other substances, to provide a stimulus which causes division and thus brings about artificial parthenogenesis. It is important to notice that the connection which in some animals exists between conjugation and reproduction is entirely a secondary one, due to conjugation being here a prelude to development. In itself conjugation is the very opposite of reproduction. The essence of reproduction is that one body becomes two. The essence of conjugation is the fusion of two bodies into one. But in most cases the germs, as we have seen, will not develop without

conjugation, which thus becomes a necessary part of reproduction in these cases. Such reproduction we have already called sexual reproduction.

(2) Another theory of the meaning of conjugation supposes that *by its means the vitality of the protoplasm is renewed*. This view is based upon certain facts that have been observed in cultures of *Paramecium*. If in a well-fed stock of this animal certain individuals and their descendants be prevented by isolation from conjugating, it will often happen that after a time they will pass into a state of "depression," in which they have an overgrown meganucleus and a stunted body, divide more slowly, and show an increasing degeneration in various organs and functions of the body. At last they are unable to digest food and die. Depression has been regarded as the old age of the stock and compared with the old age of the individual metazoan, but there are some stocks in which it does not occur, and when it does occur it can be averted, while old age cannot be averted in the metazoan. In the earlier stages of depression the animals can be artificially stimulated in such a way as to endow them with a new lease of life. This can be done by shaking the culture, or better by a change of diet, as by feeding with beef-tea. After a time the stock can be put back to a diet of hay bacteria and kept till there sets in a deeper depression, which is capable of being averted in the same way. By one means and another (after a while beef-tea failed, and brain and pancreas extracts had to be used) the life of such a culture has been kept up for two years, but the recurring periods of depression became more and more severe, and at last the whole brood died. Now comparison of the depressed cultures with similar cultures of the same stock in which conjugation is allowed shows that in the latter a period of conjugation sets in¹ shortly before depression begins in the other culture, and that in such cases depression never occurs. At first sight these facts certainly seem to point to renewal of the vigour of the protoplasm as the function of conjugation. But we have seen that there are strains of

¹ It has been said that descendants of the same exconjugant will not conjugate, and that individuals from another stock must be introduced, but this has been disproved.

Paramecium in which conjugation takes place at short intervals without any apparent connection with depression, so that if the primary object of conjugation be the same in all cases, that object would appear not to be the renewal of vitality. On the other hand there is no doubt that it has this result when it takes place in a depressed stock. In considering this it must be remembered that in *Paramecium* the process loosely called "conjugation" includes, besides true conjugation or the union of the gametes, the loss of the meganuclei (and it may be also of some part of the cytoplasm) of the conjugants. Now the meganucleus represents, as we have seen, the body-cells of the frog, and we may believe that, just as the body of the frog is subject to natural death, so the meganucleus of *Paramecium* is liable to become effete. It may well be that in both cases the germ-substance needs no revitalising, but is immortal when once it is separated from the effete part of the body, and that conjugation properly so called takes place not for the revitalising of the germs, but for some other reason. We have no means of learning from *Paramecium* whether this be so, but there are other cases which make it highly probable. Such cases are seen in *Amœba proteus*, where there is no distinction between germ-substance and body-substance and life can go on for many generations (for ever, so far as is at present known) without conjugation, and again in the parthenogenesis (p. 162) of certain higher animals, in which ova, exactly like those which in other animals are destined to conjugate, are separated from the body and develop without conjugation for an indefinite number of generations. Here at least the germ-substance stands in no need of rejuvenation. To sum up, conjugation in *Paramecium* comes on in various circumstances, among others in those which bring on depression. When it occurs in a depressed race, the latter is indeed preserved, but this is probably owing to the freeing of the germ-substance from a part of the body which has become effete. The reason of the union of the germs, in these as in other circumstances, is as obscure as ever.

(3) Another class of theories as to the meaning of this process regards it as *combining the hereditary characters of different individuals*. It is well known that the individuals

of a species of animal differ from one another in respect of each of their characters. Some will be larger, more brightly coloured, more intelligent, and so forth, than others. It is also certain that many of these differences are inherited; the children of a tall man will, for instance, be on the average taller than those of a short man. These hereditary tendencies must in some way be conveyed by the gametes, but the benefit conferred by the combination which is brought about in the zygote is the subject of more than one theory. (a) One result of the union of gametes is to produce offspring which are not exactly like either parent. It would seem that this may happen in two ways. In many cases the tendencies inherited from the two parents, when they differ, do not counteract one another, but, in respect of a given character of the animal in question, such as the size, or shape, or colour, or texture of any part of the body, one or other of the parents is *dominant*, the legacy from the other being latent or *recessive*, so that the offspring will "take after" one parent. This dominance belongs to one parent in respect of some characters and to the other in respect of others, so that every conjugation brings about a reshuffling of the characters, and the young is not exactly like either parent. In regard to other characters the tendencies inherited from the two parents do appear to counteract one another, so that by conjugation these characters of the offspring become a mean of those of the parents. In this case also there will be a difference between the two generations. Thus it comes about that no two members of a species are identical in their characters. A change in the conditions of life—as of food, temperature, enemies, and so forth—is thereby more likely to find individuals adapted to cope with it and continue the species, and this, according to one view, is the advantage derived from conjugation. (b) Another result of the conjugation of germs derived from different parents is to prevent the formation of strains descended each from a single parent. Thus, while it is continually making new kinds of individuals, conjugation is also preventing any of them from becoming permanent. It is by some held that this is of advantage, in that the members of the species are by it prevented from becoming specialised in a way that

would put them out of harmony with the conditions under which they have to live. It is possible that conjugation is beneficial to the organism in both these ways, but self-fertilisation is an obstacle to all theories which regard the consequences of the process in heredity as its primary function.

Whether or not any of these interpretations of the meaning of conjugation be the correct one, there can be no doubt that it is a process of the highest importance to the organism. If by nothing else, this is shown by the fact that the whole mechanism of sex exists only to bring it about. Sex is primarily *the differentiation of the individuals of a species into two kinds adapted to the production of two kinds of gametes*, though the differentiation may extend to other functions, such as the part played by the parents in bringing about the union of the gametes or the nourishment and protection of the young. It is an example of the physiological division of labour between individuals. The basis upon which sex is established is the unlikeness or "dimorphism" of the gametes. In *Polytoma* the two gametes are identical so far as observation shows. There is here conjugation without difference either between the gametes or between their parents. In *Paramecium* there is dimorphism of the gametes. The migratory pronucleus, which is said to be also somewhat the smaller, represents a male gamete, the stationary pronucleus represents a female gamete. The female gamete possesses the cytoplasm, the male is specialised for that part of the process which involves locomotion. These gametes, however, are produced by the same individual. Some kinds of *Hydra* are in this condition, though in them the gametes of one kind usually ripen before those of the other, so that the parent has a kind of temporary sex. In some (if not in all) species of *Monocystis* there is a dimorphism of the gametes together with a restriction of the production of each kind of them to certain individuals, which, however, show no further difference. We have here the simplest case of sex. The same thing is seen in some kinds of *Hydra* and in medusæ, where the sexes are alike in all respects both of structure and of behaviour, save that one produces only eggs and the

ther only sperm. In the frog the parents differ, not only in respect of the gametes which they form, but also in certain points of structure, such as the generative ducts and the pad upon the hand of the male, and conspicuously in their behaviour. One, the female, plays in coition the same passive part which the germs she forms play in conjugation. The other, the male, plays the active part in coition and forms germs which play the active part in conjugation. Throughout the animal kingdom it is the case that, so far as there is a difference between the sexes, the male is the active organism, the female relatively passive. It is the part of the female to lay up the surplus material that she manufactures in the formation of germs provided with the cytoplasm which the zygote will require and stocked with yolk to serve as food in the early stages of development. Sometimes, as in the hairy, warm-blooded animals known as mammals, she also nourishes the young formed from the zygote. The part of the male is freely to expend his substance in finding the female, while the germs that he forms are poor in cytoplasm, but actively motile to reach and enter the egg. In the highest animals his activity is directed also to the preservation of the female, for whom he fights and forages. It is in activity, not in size or strength or beauty, that the true difference between the sexes consists, though the female is perhaps generally the larger and the male relatively the stronger of the two, and the greater physiological vigour of the male often appears, as in the peacock and the stag, in the production of ornaments and weapons which are not found in the other sex. By this dimorphism of the parents two things are accomplished. Firstly, a division of labour of the same kind that exists between the gametes is brought about between the individuals that form them, one ensuring the union of the gametes, the other the nourishment of the zygote.¹ Secondly, it is ensured that cross-fertilisation (p. 123) shall take place, since the germs of one parent, being all of the same kind, are unable to fertilise one another.

¹ In *Vorticella*, as we have seen (p. 137), a curious imitation of sex is found. The parents are here both hermaphrodites, but they are of two kinds, of which one is active and the other is passive, as in parents which possess true sex.

Why conjugation should usually be cross-fertilisation it is hard to say, but the fact remains that as a general rule it takes place in this way, and that there are often elaborate precautions for ensuring that it should do so. The union of gametes from the same parent (which must, of course, be a hermaphrodite) is known as self-fertilisation, and it has been shown that in some cases this produces enfeebled zygotes, most of which fail to develop. On the other hand there are animals known in which self-fertilisation is the only kind of conjugation which occurs. Again, conjugation between gametes derived from near relatives, or inbreeding, is often found to be harmful—a fact which is well known to breeders, and is expressed in the marriage laws of many nations—yet in some animals it has no bad results whatever. It is perhaps safest to suppose that the advantages of conjugation, whatever they be, generally accrue in the highest degree when the gametes are not closely related. At the same time it must be remembered that gametes belonging to different species, if they will unite at all, nearly always produce a mule or hybrid which is incapable of reproducing its kind.

Cross-fertilisation.

CHAPTER XII

PLATYHELMINTHES

The Liver Fluke :
External Features.

SHEEP which are fed in damp meadows are liable to a serious and usually fatal disease known as "liver rot," in which the wool falls off, dropsical swellings appear, and the animal wastes away. This has been found to be caused by a parasite known as the Liver Fluke, *Distomum hepaticum*, which lives in the bile ducts of the sheep and sometimes of other animals, including occasionally man. It is a flat, brownish worm, about one inch long by half an inch broad, shaped like a leaf with a blunt triangular projection at the broader end. At the tip of this projection lies the mouth, in the midst of an *anterior sucker*, and just behind the projection an imperforate *posterior or ventral sucker* is placed in the middle of the ventral side and serves as a means of attachment. Nearly midway between the suckers is a smaller *genital opening*, at the hind end of the body is a minute *excretory pore*, and on the dorsal surface at about a third of the length of the animal from the front end lies the *opening of the Laurer-Stieda canal* presently to be mentioned. The body is covered with a so-called cuticle, in which little backward-pointing *spinules* are embedded.

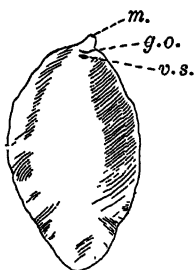


FIG. 101.—The Liver Fluke.

g.o., Genital opening; *m.*, mouth, *v.s.*, ventral sucker.

The mouth leads into an ovoid, muscular pharynx, from which a short œsophagus passes backwards to divide before

the posterior sucker into right and left branches or intestines, which run on either side of the middle line to the hind end of the body, giving off on either side many offsets, which in turn are much branched. There is no anus.

The so-called cuticle is a horny layer formed by the transformation of the epidermis or ectoderm. Below it lie successively circular, longitudinal, and diagonal layers of muscle fibres. Between this and the endoderm, which is a columnar epithelium lining the gut, lies the *parenchyma*, a meshwork of protoplasm with nuclei at the nodes and oval cells in the meshes. Muscle fibres pass across the parenchyma from the dorsal to the ventral side of the body. There are no blood vessels or coelom. It will be noticed that in the fluke a mass of tissue lies between the ectoderm and endoderm in place of the structureless lamella of *Hydra*. This is known as the mesoderm. We shall allude to it in more detail in describing the earthworm.

The excretory system

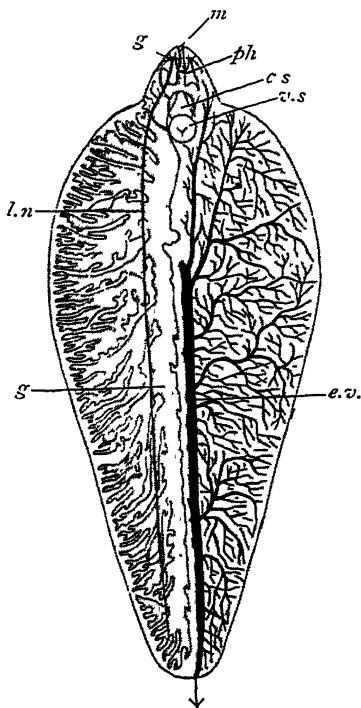


FIG. 102.—The structure of a liver fluke. —After Sommer. From the ventral surface. The branched gut (g.) and the lateral nerve (l.n.) are shown to the left of the figure, the branches of the excretory vessel (e.v.) to the right.

c.s., Position of cirrus sac; g., lateral head ganglion; m., mouth; ph., pharynx; v.s., ventral sucker. An arrow indicates the excretory aperture.

lies in the parenchyma. It consists of a meshwork of tubules joining into a main duct which lies in the middle line, from a point about a quarter of the length of the body behind its front end to the excretory pore at the hind end. The ultimate branches of the tubules are very fine and end in little structures known as *flame cells*. These are minute vesicles containing a few long cilia which keep up a flickering movement like that of a flame and drive towards the main

Excretory System.

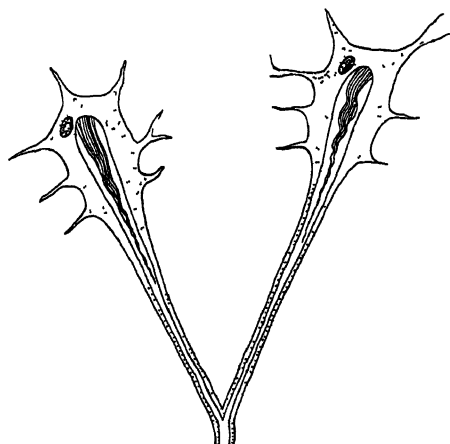


FIG. 103.—Two flame cells, highly magnified.

duct the fluid secreted into the vesicle by its walls. Each vesicle has a nucleus and may be regarded as a hollow cell. It is connected with its fellows by fine protoplasmic processes which are said to be hollow.

The nervous system consists of a collar around the pharynx with a mid-ventral swelling and a pair of lateral swellings. From these swellings or ganglia nerves are given off to the forepart of the body, and from each lateral ganglion arises a large lateral nerve cord which runs backwards below the gut to the hinder end of the body, giving off branches on the way.

Nervous System.

The liver fluke is hermaphrodite, and has very complex generative organs.

**Generative
Organs.**

The testes are two much-branched tubes lying one behind the other in the middle part of the body. The branches of each are gathered into a vas deferens, and the two vasa deferentia run forwards side by side to join, above the posterior sucker, a large, pear-shaped vesicula seminalis. From this a fine, somewhat twisted tube, the ductus ejaculatorius, passes forwards to enter a stout, muscular penis or *cirrus*, which opens at the generative pore. Normally the penis lies in a *cirrus sac*, but it can be turned inside out and thus thrust out of the pore. The ovary is a branched tubular structure on the right side in front of the testes. Its branches join to form the oviduct, which passes towards the middle line and there joins the *yolk duct*. This is formed by the union of two transverse ducts, which lead each from a longitudinal duct at the side of the body. The *yolk glands* are very numerous, small, round vesicles lying along the sides of the body and communicating by short ducts with the longitudinal ducts. The Laurer-Stieda canal is a short tube of uncertain function leading from the union of oviduct and yolk duct to a pore on the back. Possibly it is used for the reception of spermatozoa from another individual. The oviduct and yolk duct are surrounded where they join by a rounded mass, the *shell gland*, composed of numerous minute, unicellular glands. From this point the joined ducts proceed forwards as a wide, twisted tube, the uterus, to the generative opening. The uterus contains eggs, each enclosed in a shell, within which lie, besides the ovum, a number of yolk cells derived from the yolk glands, and spermatozoa. The animal is probably as a rule self-fertilised.

The life-history of the liver fluke is a very remarkable and interesting process. The eggs, which are very numerous, are laid into the bile ducts of the sheep. So long as they remain within the body of the latter they do not develop, but when they have been carried by the bile to the intestine, and thence passed to the exterior with the droppings, they will develop in damp spots if the weather be warm. In a few weeks a larva known as the *miracidium* emerges. It is conical, covered with a layer formed by five rings of big, ciliated cells, and provided with two eye-spots and two flame cells. Inside it is filled by a mass of cells. It swims by means of the cilia, with the broad end forwards. At this end there is a knob which can be thrust out as a conical spike. If it can find a member of a particular species of water snail known as *Limnæus truncatulus*¹ it works its way into the

¹ Other species of water snail are sometimes used in foreign countries.

tissues of the snail, thrusting out its spike and rotating by means of its cilia so as to bore in. Within the snail the

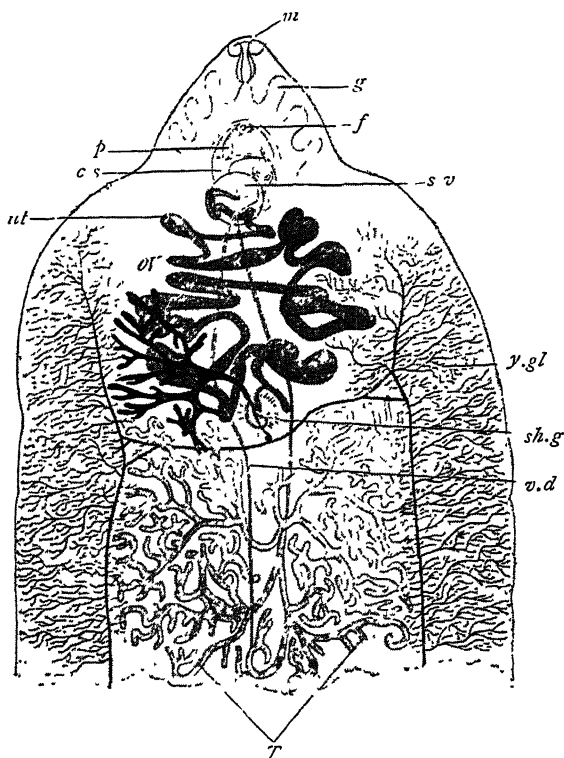


FIG. 104.—The reproductive organs of a liver fluke.
—After Sommer.

c s Cirrus sac.
f Female aperture.
g Anterior lobes of gut
m. Mouth.
ov. Ovary (dark).
p Penis.

s v Seminal vesicle
sh g Shell gland.
T. Testes (anterior)
ut. Uterus.
v d Vas deferens.
y.gl Diffuse yolk glands

cilia are lost and the larva increases in size and grows into a hollow sac or *sporocyst*. Sometimes this multiplies by

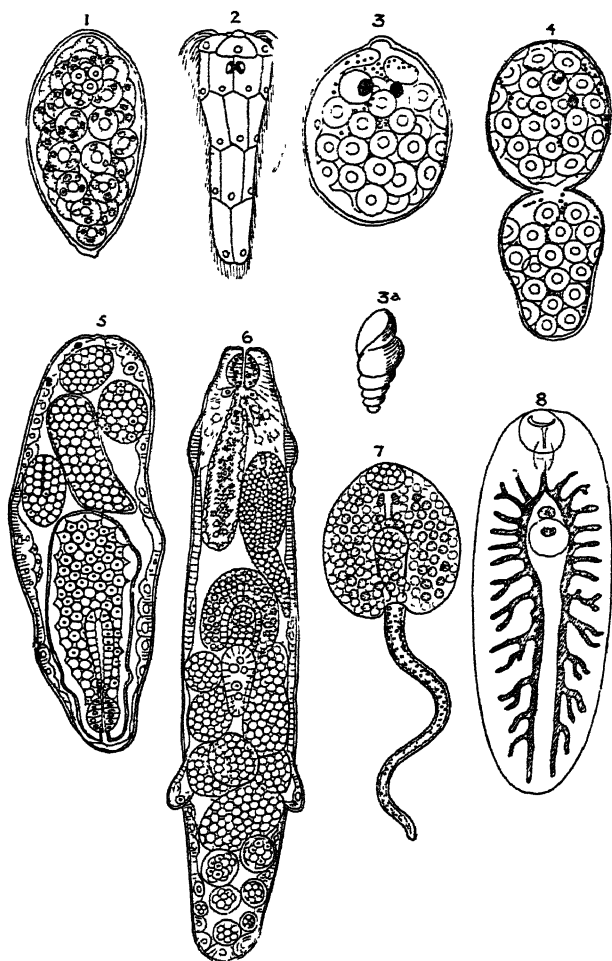


FIG. 105.—The life-history of a liver fluke.—After Thomas.

1. Developing embryo in egg-case; 2. free-swimming ciliated embryo;
3. sporocyst; 3a. shell of *Limnaeus truncatulus*; 4. division of sporocyst; 5. sporocyst with rediae forming within it; 6. redia with more rediae forming within it; 7. tailed cercaria; 8. young fluke.

dividing transversely. Within the sporocyst some of the cells lining the cavity behave like parthenogenetic ova, dividing to form a blastula, which invaginates to give rise to a two-layered sac or gastrula. This grows into another form of larva, the *redia*, which bursts out of the sporocyst and migrates, usually into the liver of the snail. The rediæ devour the tissues of the snail and finally kill it. Each redia has an elongated body with an anterior mouth, a muscular pharynx, and a short, sac-like gut. A little way behind the pharynx the body-wall is thickened to form a muscular collar, and not far from the hind end are two blunt conical processes on one side. Posteriorly there is a large body cavity lined by an epithelium like that of the cavity in the sporocyst. Cells derived from the wall of the body cavity develop in much the same way as in the sporocyst and give rise to daughter rediæ, which escape from the parent by an opening behind the collar. Several generations of rediæ usually succeed one another thus, but eventually they cease to produce daughters of their own kind, and give birth instead to creatures known as *cercariæ*, with a flat, heart-shaped body, two suckers, a forked gut, and a tail. The cercaria emerges from the redia, works its way out of the snail, and swims by means of the tail. Soon it settles upon a blade of grass, loses its tail, secretes around itself a cyst by means of special *cystogenous cells* of the ectoderm, and waits till the grass is eaten by a sheep. In the gut of the latter the cyst is digested and the cercaria, making its way up the bile duct, grows into an adult fluke.

It will be seen that in this life-history we have a case of alternation of generations far more complicated than that of *Obelia*, and differing from the latter also in that not sexual and truly asexual, but sexual and parthenogenetic generations succeed one another. The former kind of alternation of generations is known as *metagenesis*, the latter as *heterogamy*. It should also be noticed that there are three kinds of individual involved in the cycle. The life-history of the liver fluke is shown by a diagram in Fig 106.

The liver fluke belongs to a group of animals known as *Platyhelminthes*. These are flat, bilaterally symmetrical worms, without anus, blood vessels, or body cavity in the adult, with an excretory system formed of branched tubes

ending in flame cells, and with a complicated system of reproductive organs. Some of them, known as **Platyhelminthes**. *Turbellaria*, lead a free life, and are ciliated all over. Others, like the liver fluke, are parasitic and covered with a cuticle, and possess suckers. These are known as *Trematoda*.

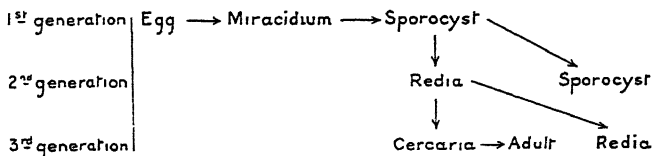


FIG. 106.—A diagram of the life-history of the liver fluke.

To the Platyhelminthes belong also the *Tapeworms or Cestoda*, of which *Tænia solium*, found in man, is an example. In the adult state this worm may reach a length of many feet. It lives in the intestine, to whose wall it is attached by a head or *scolex*, provided with four suckers and a crown of hooks. Behind the head is a

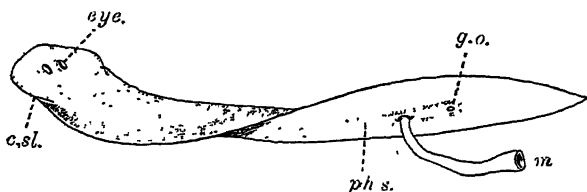


FIG. 107.—A turbellarian (*Planaria polychroa*) swimming.—From Shipley and MacBride.

c.sl., Ciliated slit at side of head; *eye*; *g.o.*, genital opening, *m.*, mouth, at end of outstretched pharynx; *ph.s.*, sheath into which pharynx can be withdrawn

narrow neck, followed by a long chain of joints or *proglottides* which it buds off. The younger of these, near the head, are small, but they grow larger as they are pushed farther from the head by the formation of new joints. The body is covered with a cuticle, under which lies a layer of very deep cells with longitudinal muscle fibres between them and a circular layer of muscle below them. Inside

this is a mass of parenchyma like that of the fluke, in which are embedded the excretory, generative, and nervous systems. There is no alimentary canal, nutriment being absorbed

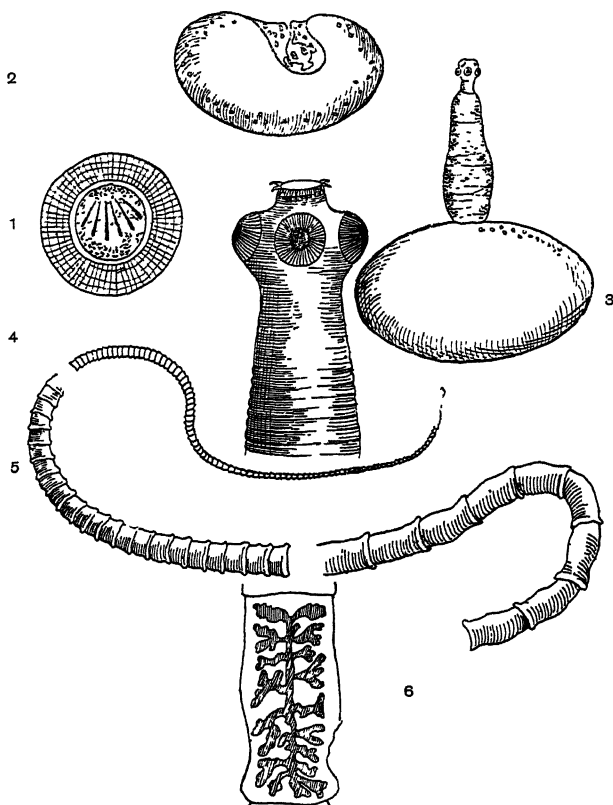


FIG. 108.—The life-history of *Tania solium*.—After Leuckart.

1. Six-hooked embryo in egg-case; 2. proscotex or bladder-worm stage, with invaginated head; 3 bladder-worm with evaginated head; 4. enlarged head of adult, showing suckers and hooks; 5. general view of the tapeworm, from small head and thin neck to the ripe joints; 6. a ripe joint or proglottis with branched uterus; all other organs are now lost.

through the surface of the body. The excretory system is of the same type as that of the fluke, with flame cells and a larger and a smaller main duct on each side, connected by a transverse vessel on the hinder side of each proglottis. In the last proglottis these vessels open by a median pore. The nervous system consists of a ring in the head with small forward nerves and two lateral nerve cords. The reproductive organs have the same general structure as in the liver fluke; they

are shown in Fig 108. A complete set of them is found in each proglottis. Apparently each joint fertilises itself. From time to time the last proglottis breaks off, singly or with others, and passes out of the intestine to the exterior. It has some power of independent movement by contraction of its muscles. The eggs are set free by its rupture. If, as may happen in various circumstances, they are now swallowed by a pig, their shells

are dissolved in its alimentary canal and a little spherical *six-hooked embryo* or *onchosphere* is set free from each. This bores its way from the intestine of the pig into its blood vessels and is carried to the muscles and other organs, where it loses its hooks, increases in size, and becomes a *bladder-worm* or *cysticercus*. The wall of this becomes tucked in at one spot, forming a pouch, on the inner wall of which the suckers and hooks of the future head appear. No further change takes place unless the flesh of a pig infested with such bladder-worms (known as "measly" pork) be

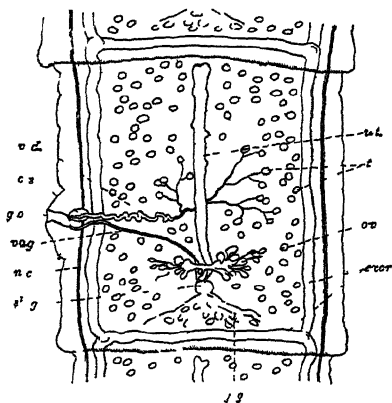


FIG 109 —A proglottis of *Tiznia solium* with the reproductive organs at the stage of complete development

c s Cirrus sac *excr* excretory canals *g o* genital opening *n c* nerve cord *ov*, ovary *s h g*, shell gland *t* testes *v d* vas deferens *v a g*, vagina *y g*, yolk gland

eaten raw or "underdone" by man. When this happens, the stimulus of the new surroundings causes the head to be turned inside out. The bladder is digested, but the head fixes itself and begins to bud off proglottides. The life-history of *Tenia solium* may be summed up as follows:—

Egg→Onchosphere→Cysticercus→Scolex→Adult.

It will be seen that only one generation is involved, unless each proglottis be regarded as a complete individual,

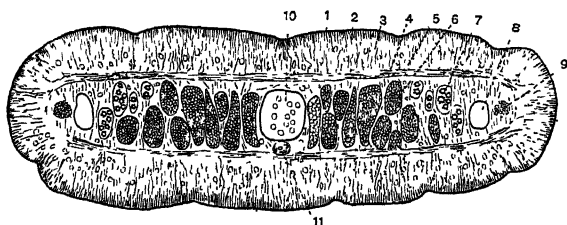


FIG. 110.—A transverse section through a proglottis of *Tenia* in which the reproductive organs are well developed.—From Shipley and MacBride.

- 1, Cuticle; 2, long-necked cells of ectoderm; 3, longitudinal muscle fibres cut across, 4, layer of circular muscles; 5, split in the parenchyma which lodges a calcareous corpuscle; 6, ovary; 7, testis with masses of male germ-mother-cells forming spermatozoa; 8, longitudinal excretory canal; 9, longitudinal nerve cord; 10, uterus; 11, oviduct.

and not merely as a part of the parent body broken off to carry the eggs.

Other common tapeworms are: *Tenia saginata*, without hooks, found in man, with the bladder-worm stage in the ox; *T. serrata* in the dog, with a bladder-worm in rabbits, hares, and mice; *T. cœnurus* in the dog, with the bladder-worm known as *Cœnurus cerebralis* in the brain of sheep and other hoofed animals, where it causes "staggers"; and *T. echinococcus* in the dog, with the bladder-worm *Echinococcus* in sheep, oxen, pigs, and sometimes in man. The latter two species produce in the bladder-worm stage numerous heads. Since only one of these can be regarded as continuing the individuality of the

Other Tapeworms.

bladder-worm, the others must be looked upon as buds from it, so that there is here a metagenesis.

The tapeworm and the liver fluke, like *Monocystis*, are parasitic animals. An organism is said to be **Parasitism.** parasitic when it obtains its nourishment from the body of another living organism, with which it dwells,

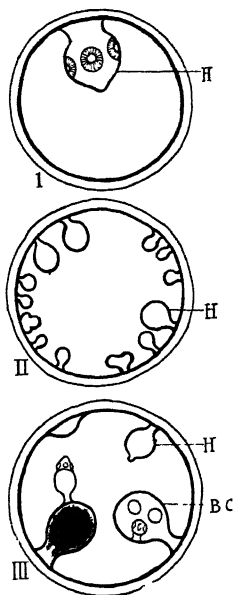


FIG. III.—Diagrams of bladder-worms.

- I. The ordinary *Cysticercus* type, with one head (*H*).
- II. The *Cœnurus* type, with many heads.
- III. The *Echinococcus* type, with many heads, and with brood capsules producing many heads.

without conferring any benefit in return. The organism from which a parasite derives its nourishment is known as its *host*. The examples we have studied show various features which are common in parasitic animals. They are sluggish, and have no external organs of locomotion, since they do not need to travel in search of food or to avoid

enemies ; they have usually organs of fixation, and by the formation of very numerous offspring they provide against the inevitable failure of most of the young to find a host. In many cases their distribution is aided and the young nourished by entering a second host, and this results in very remarkable life histories. Parasites may be *external*, as in the case of the flea, or *internal*, as in the examples given above.

CHAPTER XIII

ANNELIDA: THE EARTHWORM, NEREIS

ALMOST everywhere in England earthworms are found.

Habits. They live usually in the upper layers of the soil in burrows, which they make partly by boring with the pointed front ends of their bodies, partly by swallowing the earth in front and passing it out behind, in which case the earth which is passed out forms the well-known "worm casts." The sides of the burrow are lined with a slime secreted by unicellular glands in the skin, and if the opening is not protected by a worm cast it is usually

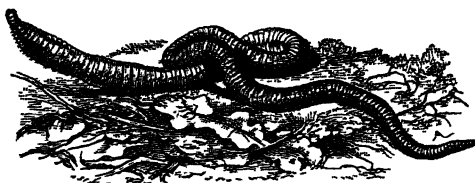


FIG. 112.—The Earthworm.

closed by leaves or small stones. Such leaves may often be seen sticking up from the ground, and will be found to have been pulled into the burrow skilfully, with the narrowest part foremost. At night, if the weather be warm and not too dry, the worms will stretch themselves out of their holes, keeping the hinder end of the body fixed in the opening, so that they can pull themselves back at once if danger threatens. In dry weather or hard frost they burrow deep and retire to a small chamber, which they line with little stones. In wet weather they are sometimes flooded

out, but they rarely leave their burrows in other circumstances, except when they are about to die owing to the attacks of the parasitic maggots of certain flies. The food of earthworms consists of the organic matter in the soil, which they swallow, and of leaves both fresh and decaying. They will also eat animal matter, and are said to be very fond of fat. Charles Darwin has shown the remarkable effects which these insignificant creatures have upon the surface of the earth. By making the soil more porous they expose the underlying rocks to the disintegrating action of water, by solution owing to the presence of carbon dioxide and other acids of the soil, and by frost, and the small stones which eventually result from this action are made still smaller by friction and solution within their bodies. Thus they help in the formation of the soil. At the same time they are aiding in its removal. Their castings dry and crumble, and are blown about by the wind or else are washed down by the rain. On sloping ground this fine material tends to be carried away downwards, and thus the denudation of hills is largely due to the action of earthworms. On the other hand, their work is highly beneficial to the farmer. The soil is by them thoroughly mixed, submitted to the action of the air, and constantly supplied with a fine "top dressing." It has been calculated that earthworms bring up annually a layer of soil one-fifth of an inch in thickness, which is spread by the weather in the way we have described. Organic matter is converted into a useful form and amalgamated with the earth, and the latter is made easier of penetration by the roots of plants.

The commonest English earthworm is *Lumbricus herculeus*.

External Features. The body of this animal is roughly cylindrical, but pointed in front and broadened behind. It reaches a length of seven inches. There is no distinct head, but a lobe known as the *prostomium* overhangs the mouth, which is a crescentic opening on the lower side of the front end. The body is divided into a series of rings or *segments*, and at the hinder end is the terminal *anus*. The first segment is known as the *peristomium* and the mouth lies between it and the *prostomium*. On the dorsal side, the latter projects across

the peristomium¹ There are about 150 segments At about one-third of the length of the body from its front end, in segments 32-37 inclusive, a glandular thickening of the epidermis lies athwart the back like a saddle and is often mistaken for the scar of a wound This is known as the *clitellum* The skin of the worm is brownish above and paler below, it is covered with a fine, tough, iridescent cuticle secreted by the underlying cells In every segment except the first and the last there are eight bristles or *setae*, placed in two pairs on each side, a *lateral pair*, placed slightly above the middle of the side, and a *ventral pair* between the lateral and the mid-ventral line The *setae* can be felt with the fingers, they are embedded in sacs of the epidermis, by which they are secreted, and to these sacs are attached muscles, by which they can be moved The *setae* are organs of locomotion The worm extends its body with the bristles withdrawn Then it thrusts out those of the forepart, so that they catch in the soil and hold firm while

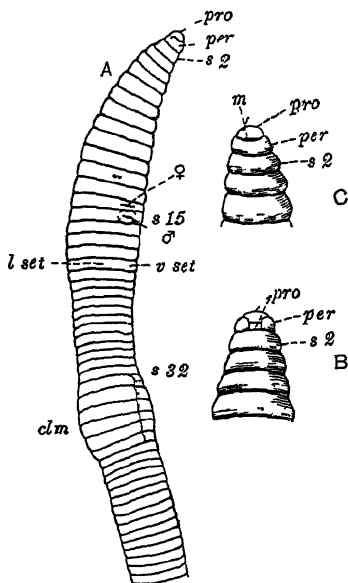


FIG 113 —A, The forepart of the body of an earthworm (*Lumbricus terrestris*), from the right side, B, the first five segments from below, C, the same from above

clm Clitellum l set lateral setae m, mouth per, peristomium pro, prostomium s 2 s 15 s 32 second fifteenth and thirtieth somites or segments, v set ventral setae, ♂, opening of vas deferens ♀ opening of oviduct

¹ In the related *Allolobophora* the prostomium reaches only half way across the peristomium

the hinder region is being drawn up. A wave of movement of this kind passes down the body. The ventral setæ of the clitellum, of the twenty-sixth, and of the tenth to the fifteenth segments are straighter and more slender than those of other segments, which are stout and somewhat hooked. This modification is in connection with the use of the setæ of the twenty-sixth segment during coition, and of the other straight setæ during the formation of the cocoon in which the eggs are laid.

A number of internal organs open separately upon the surface of the body. We have already mentioned the mouth and anus. The *openings of the vasa deferentia* are a pair of slits with swollen lips found on the under side of the body in segment 15. In front of them, in segment 14, are the two small *openings of the oviducts*. The *spermathecal pores*

**External
Openings.**

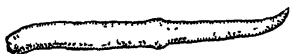


FIG. 114.—One of the ordinary setæ of an earthworm, removed from the seta sac and magnified.

are two pairs of small, round openings in the grooves between segments 9-10 and 10-11 at the level of the lateral setæ. The *nephridiopores* are openings which lead from the excretory tubes or nephridia. They

are found, as a pair of minute pores in front of the ventral setæ, in each segment except the first three and the last. The *dorsal pores* are small, round openings on the mid-dorsal line in the grooves between the segments. The first is behind the eighth segment, and there is one in each subsequent groove. They open into the body cavity.

The body of the worm may be said to consist of two tubes, one within the other. The inner tube is the gut, the outer the body-wall. Between the two lies the coelom or body cavity, divided into compartments by a series of *septa*, which reach from the gut to the body-wall, where they are attached opposite the grooves on the surface of the body. The coelom contains a fluid in which float leucocytes. The *body-wall* is covered by the *cuticle*. Under this lies the *epidermis*, an epithelium consisting of columnar cells, many of which are glandular or sensory, with small cells between their bases. The cuticle

Body-wall.

is perforated by a pore over each gland cell. The epidermis of the clitellum consists of several layers of gland cells. Below the epidermis is a *circular layer of muscle*, consisting of unstriated fibres running around the body, and below this again lies a much thicker *longitudinal layer of*

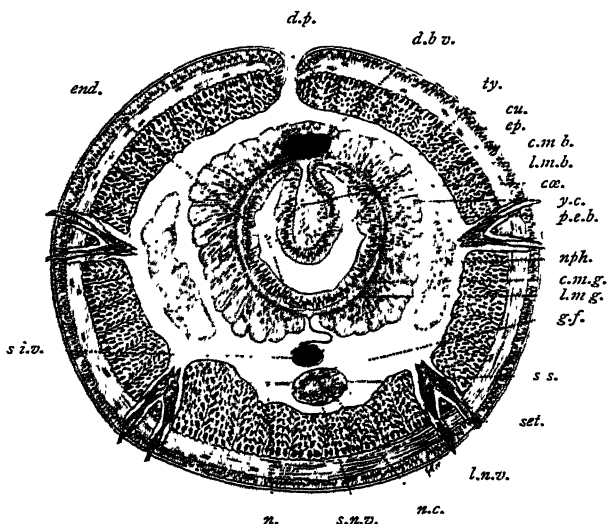


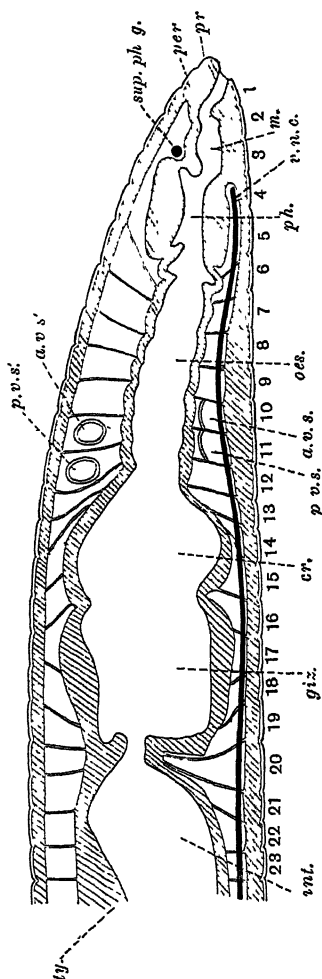
FIG. 115.—A transverse section through an earthworm in the region of the intestine.

cæ., Coelom; c.m.b., circular muscle of body-wall; c.m.g., circular muscle of gut; cu., cuticle; d.b.v., dorsal blood vessel; d.p., dorsal pore; ep., epidermis; end., endoderm; g.f., giant fibres; l.m.b., longitudinal muscle of body-wall; l.m.g., longitudinal muscle of gut; l.n.v., lateral neural vessel; n., nerves; n.c., nerve cord; nph., nephridium; p.e.b., peritoneal epithelium of body-wall; set., seta; s.i.v., subintestinal blood vessel; s.n.v., subneural blood vessel; s.s., seta sac; ty., typhlosole; y.c., yellow cells. Seta sac muscles are shown but not lettered.

muscle, composed of similar fibres running along the body and placed in rows at right angles to the surface, supported by connective tissue. Within the longitudinal muscle is the coelomic epithelium, which is here a layer of pavement cells lining the body cavity.

The alimentary canal is straight. It begins with a short,

wide, thin-walled mouth or buccal cavity in the first three segments, which leads into a structure with thick muscular



walls known as the pharynx.

This lies in front of the septum between the fifth and sixth segments, but pushes the latter backwards as far as the seventh. Numerous strands of muscle run from it to the body-wall. Behind it lies the oesophagus, a straight, narrow, thin-walled tube, which extends to the fourteenth segment. In the eleventh segment it bears at the sides a pair of *oesophageal pouches*, and in the twelfth two pairs of *oesophageal glands*. These contain large cells which secrete calcium carbonate and pass it through the pouches into the oesophagus. In the fifteenth

FIG. 116.—A diagram of a longitudinal section of an earthworm.

a.v.s. Anterior vesicula seminalis.
a.v.s'. Posterior lateral horn of the same overhanging the oesophagus.

cr. Crop
giz. Gizzard.
int. Intestine.
m. Mouth.
oes. Oesophagus.
p.v.s. Posterior vesicula seminalis.
p.v.s'. Horn of the same overhanging the oesophagus.
per. Peristomium.
ph. Pharynx.
pr. Prostomium.
sup ph.g. Suprapharyngeal ganglion.
ty. Typhlosole.
v.n.c. Ventral nerve cord.
1-23. Segments.

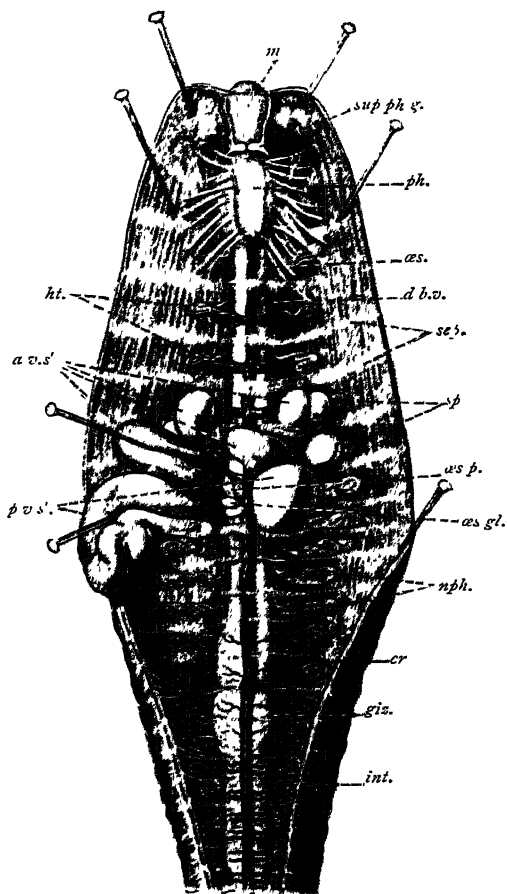


FIG. 117.—An earthworm (*L. herculeus*), dissected from above.

a v. s., Horns of the anterior vesicula seminalis; *cr.*, crop; *d. h. v.*, dorsal blood vessel; *giz.*, gizzard; *ht.*, hearts; *int.*, intestine; *m.*, mouth; *neph.*, nephridia; *æs.*, oesophagus; *æs. gl.*, oesophageal glands; *æs. p.*, oesophageal pouch; *p. v. s.*, horns of the posterior vesicula seminalis; *ph.*, pharynx; *sep.*, septa; *sp.*, spermathecae; *sup ph. g.*, suprapharyngeal ganglia.

and sixteenth segments the oesophagus expands into a large, thin-walled *crop*, which in turn communicates behind with the *gizzard*, another swelling, with thick muscular walls and a horny lining, in segments 17 and 18. From the gizzard to the anus runs a wide, thin-walled tube known as the intestine. The intestine is narrowed where it passes through the septa, and its dorsal wall is infolded to form a longitudinal ridge known as the *typhlosole*. The gut is lined with a layer of columnar epithelium, outside which are thin longitudinal and circular muscular layers, covered by the coelomic epithelium, which here consists of the *yellow cells*. These are large and contain yellow granules of an excretory product. They fall off into the coelomic fluid, and there break up and set free their granules. The typhlosole is filled with yellow cells.

Food is drawn into the mouth by a sucking action of the muscular pharynx, passed along the oesophagus, stored in the crop, ground up in the gizzard with the aid of small stones which have been swallowed, and in the intestine first digested by juices secreted from the epithelium, and then absorbed. The surface for these purposes is increased by the presence of the typhlosole. The function of the secretion of the oesophageal glands is uncertain. It has been supposed to be an excretion of the calcareous matter, which is very plentiful in the dead leaves, of which the food is largely composed. Probably it has some further function, whether this be the neutralisation of the acids of the food, or, as seems to be the case, the removal of carbon dioxide in the form of calcium carbonate.

The earthworm has a well-developed central nervous system which consists of (1) a pair of *supra-pharyngeal ganglia*, rounded bodies lying above the mouth, and sometimes known together as the *brain*, (2) two slender *circumpharyngeal commissures* running from these round the pharynx, and (3) a *ventral nerve cord* which starts from the commissures between the third and fourth segments and runs the whole length of the body in the coelom below the gut, swelling into a ganglion in each segment. The first of these ganglia is bilobed and is known as the *subpharyngeal ganglion*. Nerves are given off to the prostomium from the supra-

**Nervous
System.**

pharyngeal ganglia, and to the first two segments from the commissures, and the ventral cord gives off three pairs of nerves in each segment. The forepart of the alimentary canal receives nerves from the circumoesophageal commissures. Though the ventral cord appears to be single, it is really double, and can be seen in transverse sections to be divided into right and left halves by connective tissue. Transverse sections also show that the middle and upper part of the cord consists of fine longitudinal nerve fibres and the lower and outer part of nerve cells. Above the mass of fine longitudinal fibres are three bundles of such fibres, each bundle being enclosed in a sheath and known as a *giant fibre*. The nerves consist of afferent fibres, which start in sense cells of the epidermis and end as a bunch of fibrils in the central nervous system, and efferent fibres, which start from nerve cells in the ganglia and end against muscle and other cells.

An earthworm has no well-developed organs of sense, but certain of the

columnar cells of the epidermis are rod-shaped and prolonged at their inner ends into fibres, which run in the nervous system (Fig. 119). These are sense cells, and in the forepart of the body some of them are collected into groups, which are rudimentary sense organs. Experiment shows that the worms are sensitive to light and to vibrations of the ground and can smell, but gives no evidence of a sense of hearing.

The excretory organs of an earthworm, like those of the

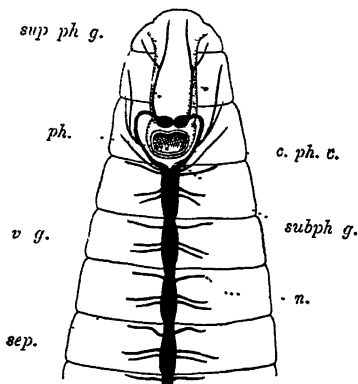


FIG. 118.—A diagram of the forepart of the nervous system of the earthworm.

c. ph. c., Circumpharyngeal commissure; *n.*, nerves; *ph.*, pharynx cut through; *sep.*, septa; *subph. g.*, subpharyngeal ganglia; *sup. ph. g.*, suprapharyngeal ganglia; *v. g.*, ganglia of ventral cord.

frog, consist of tubes whose walls are excretory and richly supplied with blood vessels, but the tubes, instead of being collected into compact kidneys, are distributed along the body, one pair to each segment, except the first three and the last. Each tube or *nephridium* is

Excretion.

The nephridium begins as a kidney-shaped funnel or *nephrostome* hanging from the front side of a septum near the nerve cord. The nephrostome consists of a large crescentic

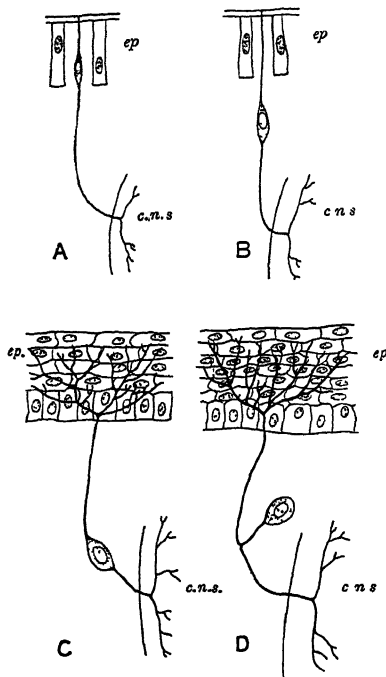


FIG. 119.—A diagram showing the mode of ending of the sensory nerve fibres of the earthworm and the relation of this type to that which is found in most of the sensory fibres of the frog. See also Fig. 48.

A, The arrangement found in the earthworm; B, that of the worm *Nereis*; C, that of a fish; D, that of a frog or man.

c.n.s., Ending of the neuron in the central nervous system; ep., ending in the epidermis.

central cell with a rim of marginal cells around it arranged so as to surround a crescentic, funnel-shaped opening, turned to one side. The funnel is ciliated, and from it there leads backwards a narrow, ciliated tube. This passes through the septum to the main part of the nephridium, which lies behind the septum in the coelom of the next segment, opening to the exterior by the nephridiopore in this segment. The narrow part of the tube is

long and winding and loses its cilia in places. It is followed by a wider, short, brown region, ciliated throughout, this by a still wider tube which is not ciliated, and finally a short, very wide, muscular tube leads to the nephridiopore. The whole tube, except the muscular region, is formed of hollow cells shaped like drain pipes

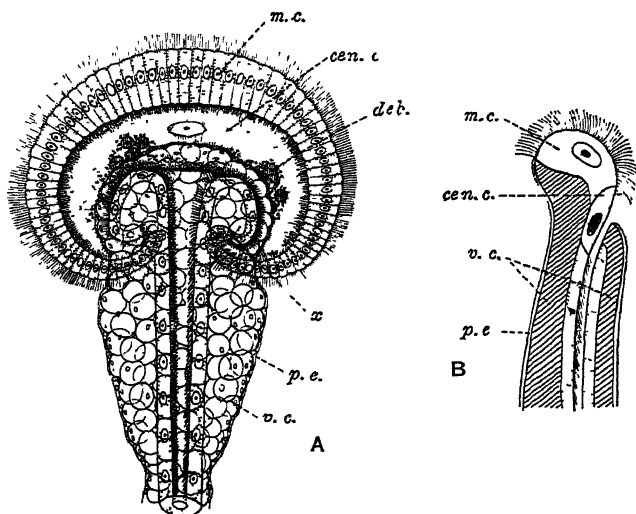


FIG. 120.—The nephrostome or funnel of a nephridium of the earthworm: *A*, in surface view, highly magnified; *B*, in longitudinal section, diagrammatic.

cen.c., Central cell; *deb.*, debris of coelomic corpuscles and excretory granules being swept into the funnel; *m.c.*, marginal cells; *p.e.*, peritoneal epithelium; *v.c.*, vesicular connective tissue cells; *x.*, point at which the marginal cells join the lining of the tube, which turns over round the opening.

and set end to end. The cilia set up a current which sweeps in and carries off the excretory granules formed by the yellow cells, together with substances taken from the blood and excreted by the walls of the tubes. Some of these, in the form of granules, colour the brown part of the tube. Earthworms have no special *respiratory organs*, but an interchange of gases with the air takes place in the skin, which is richly supplied with blood vessels.

The blood of an earthworm is red on account of the presence of hæmoglobin, which is in solution, not in corpuscles. Colourless corpuscles are present. The blood-vascular system is very complicated. Its main outlines are as follows. A large *dorsal vessel* runs the whole length of the body from the hinder

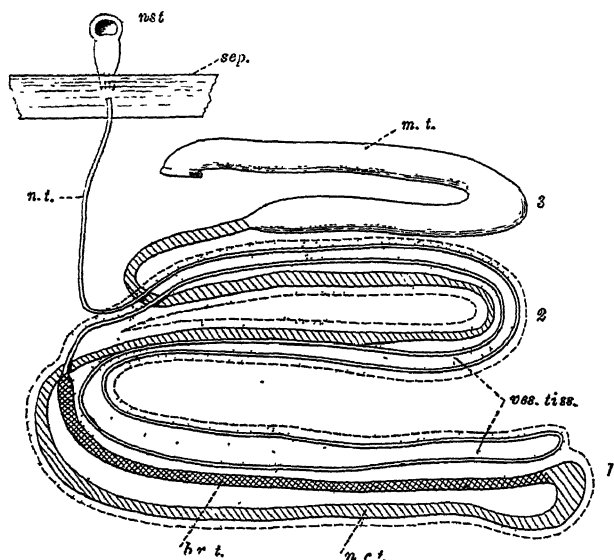


FIG. 121.—A diagram of a nephridium of the earthworm.

br.t., Brown, ciliated tube; *mt.*, muscular tube, *nc.t.*, glandular, non-ciliated tube, *nt.*, narrow tube, ciliated in parts; *nst.*, nephrostome, *sep.*, septum; *ves. tiss.*, connective tissue with vesicular cells and blood vessels, 1, 2, 3, the three banks of the tube.

end to the pharynx. It is contractile, and in it the blood is driven forwards. This vessel supplies blood to, and receives it from, the gut directly and the rest of the body indirectly. It communicates by many small vessels with the intestine and by two large vessels in the tenth segment with the œsophagus, and ends in front by breaking up into branches which supply the pharynx. In each of the segments 7-11 it gives off a pair of large contrac-

tile vessels or *pseudo-hearts*. These encircle the oesophagus and join a *ventral or subintestinal vessel* which hangs by a mesentery below the gut. In the pseudo-hearts the blood flows downwards from the dorsal to the ventral vessel, and in the latter it flows backwards. From the ventral vessel the blood passes along branch vessels partly to the nephridia and partly to the skin. Purified by these organs, it is returned along various paths to the dorsal vessel. Among the subsidiary vessels are a *subneural* and two *lateral neural vessels*, in which the blood flows backwards, and *parietal vessels*, of which a pair in each segment of the intestinal region of the body connect the subneural with the dorsal vessel. The main blood vessels of the earthworm cannot

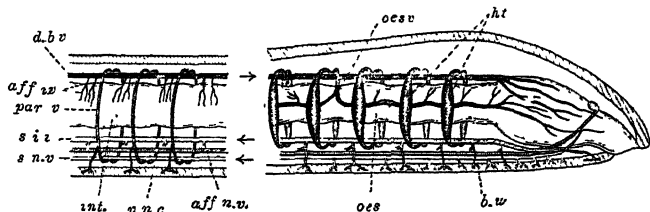


FIG. 122.—A diagram of the blood-vascular system of the earthworm.

aff.i.v., Afferent vessels of the intestine; *aff.n.v.*, afferent vessels of the nephridia; *b.w.*, body-wall; *d.b.v.*, dorsal blood vessel; *ht.*, pseudo-hearts; *int.*, intestine; *oes.*, oesophagus; *oes.v.*, oesophageal vessel; *par.v.*, parietal vessel; *s.i.v.*, subintestinal vessel; *s.n.v.*, subneural vessel; *v.n.c.*, ventral nerve cord.

be distinguished into arteries and veins, but their ends are joined by capillaries.

Earthworms are hermaphrodite, every individual having a complete set of organs of each sex. The *female organs* include the ovaries, oviducts, and spermathecae. The ovaries are two small, pear-shaped bodies hanging into the coelom of the thirteenth segment from the septum in front of it. Each ovary is a local thickening of the coelomic epithelium. The broad end of the pear is attached to the septum and contains a fused mass of unripe ova. Maturation divisions take place at the base of the stalk, which contains the ripe eggs. These fall from it into the body cavity and are taken up by the oviducts, which open by wide funnels into the coelom in the thirteenth

segment, pass through the septum behind, and open to the exterior in the fourteenth. In the latter segment, each bears a swelling, the *receptaculum ovarum* or *egg sac*, in which the eggs are stored. The *spermathecae* are two pairs of small, round sacs which lie in the ninth and tenth segments and open in the grooves behind them. Their function is to receive sperm from another worm. The *male organs* consist of testes, vesiculæ seminales, and vasa deferentia. The testes are two pairs of small, flat, finger-lobed bodies attached to the hinder side of the septa in

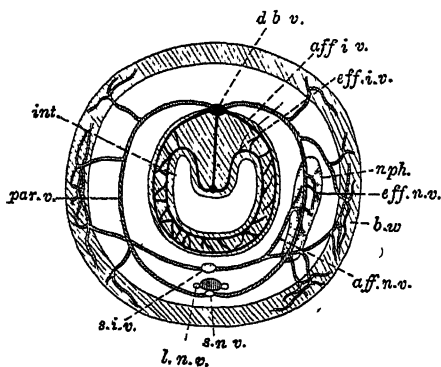


FIG. 123.—A diagram of a transverse section of the earthworm in the intestinal region to show the arrangement of the blood vessels. Lettering as in Fig. 122.

front of segments 10 and 11. They are local thickenings of the coelomic epithelium like the ovaries, to which they correspond in position. The testes bud off cells known as *sperm-mother-cells*, which give rise to spermatozoa in the vesiculæ seminales. The latter are large sacs, formed by

of parts of the coelom, which enclose the testes. Each consists of a median part and lateral horns. The anterior vesicula seminalis, in segment 10, has four lateral horns, two in front and two behind, which push out the septa and bulge into the ninth and eleventh segments. The posterior vesicula seminalis, in segment 11, has only two such horns, which project into the twelfth segment. Each sperm-mother-cell forms by multiple fission, in the course of which the usual reduction division takes place, a mulberry-like mass (Fig. 76, 1) consisting of little cells attached to a central mass of residual protoplasm known as

the *cytophore*, by which they are nourished. The little cells become pear shaped, with the broad ends on the cytophore, gradually increase in length, and change their shape till the mulberry has become a tuft of threads, each thread being a spermatozoon with a very slender head. Finally the spermatozoa break loose. In the median part of each vesicula seminalis, directly behind the testes, is a pair of large ciliated funnels with folded walls, known as *sperm rosettes*. These funnels lead into the vasa deferentia, which the two on each side join and pass backwards to open on segment 15. The cilia of the rosettes draw the ripe sperm into the ducts.

Pairing takes place at any time from spring to autumn in warm, damp weather. Two worms stretch themselves out of their burrows and place their ventral sides together with the heads pointing in opposite directions, their bodies being held together by a substance secreted from the clitella. Sperm is passed from the vas deferens of each worm into the spermathecae of the other, after which the worms separate. The eggs are laid in a cocoon, which is secreted by the clitellum as a broad band round the body and passed forwards over the head. The cocoon contains a nutrient fluid,

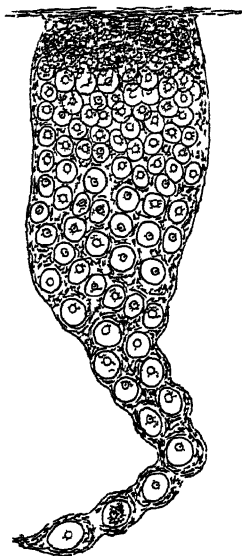


FIG 124 —One of the ovaries of an earthworm

and into it sperm which has been received from another worm is transferred in a little packet or spermatophore. In passing over the head the ends of the elastic cocoon close, and it becomes a small, lemon shaped body, which is left in the earth. Each cocoon contains three or four ova, which are fertilised in it, but usually only one completes its development.

muscles, excretory and generative organs, and so forth. These tissues are together known as the *mesoderm*, and animals which possess this third layer are known as *Triploblastica*, while those, like *Hydra*, which possess only two are *Diploblastica*. Both in the earthworm and in the frog the mesoderm contains spaces of two kinds, the *cœlom* or body cavity and the *hæmocœle* or blood vessels. The functions of the *cœlom* are threefold. (1) It forms a *perivisceral space*, which surrounds the principal viscera and gives room for their movements. (2) From its walls are derived the generative cells. This is clearly seen in the case of the ova, which are shed into the perivisceral cavity, but it is less clear in the case of the spermatozoa, because these are passed into special vessels. (3) It is concerned in excretion. In an earthworm, where the yellow cells of its walls form excreta which are removed by the nephridia, this is more obvious than in the frog, but the latter possesses in the tadpole stage (and, according to some authorities, also in the adult) funnels which, like those of the nephridia of the earthworm, pass *cœlomic* fluid into the excretory tubules, where it serves to wash out the waste products. The *hæmocœle* is a system of spaces of more complex form than the *cœlom*. Its function is to contain the blood and transfer it from place to place in the body. A blood-vascular system is made necessary in most triploblastic animals by the presence of the great mass of internal tissues which constitute the mesoderm.

Another feature of the morphology of an earthworm to which attention must be called here is its **Segmentation.** *segmentation*. We have seen that merism or the repetition of parts is universal among animals. In an earthworm the whole body consists of similiar divisions arranged one after the other in a line or series. These divisions are the segments. Each contains a ring of the body-wall, with setæ and openings, a separate portion of the *cœlom*, a section of the gut, a ganglion, nephridia, and blood vessels. A body so constructed is said to be *metamerically segmented*. Most of the segments resemble one another closely, but in the forepart of the body they show considerable differences in the reproductive, alimentary, and other organs. The body of an earthworm is composed

of similar divisions, because all the organs are repeated together at regular intervals. There are other animals in which only some of the organs are thus repeated, as in the frog, where the vertebræ, nerves, and to some extent the muscles exhibit segmentation, so that the regions of which the body might be regarded as composed are much less alike than they are in the earthworm. In such cases segmentation is said to be incomplete. The tapeworm presents an example of a kind of segmentation which is very complete, but is of

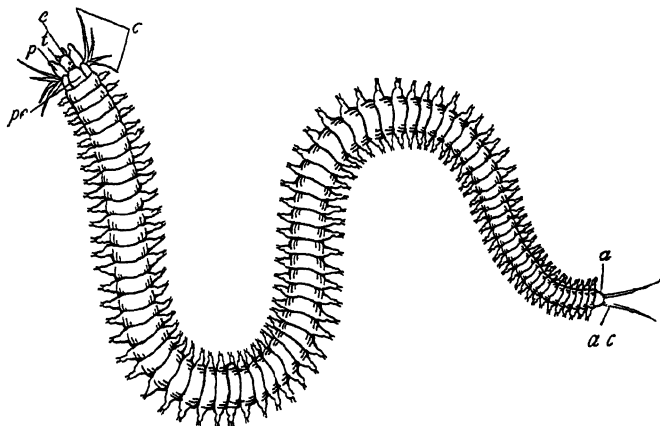


FIG 126 —*Nereis cultrifer* —From Thomson

a, Anus *ac*, anal cirri *c* tentacular cirri *e*, eyes *p*, palp
pe, peristomium *t*, tentacles

quite a different nature from that of the earthworm, the youngest segments being at the front end and the old ones dropping off, whereas in the earthworm the youngest segments are those at the hind end and the animal does not shed its segments.

The earthworm is adapted to a burrowing habit and a vegetarian diet. Many marine worms, however, while they resemble the earthworm in most respects, lead a free and predaceous existence. Of these, *Nereis cultrifer*, common under stones on the south coast of England, where it is known as the Red Cat, is a

good example. The body of this worm is about six inches in length, of a greenish colour, roughly cylindrical, tapering towards the hinder end, and divided into about eighty segments. Like the earthworm, it is covered with a thin cuticle and provided with setæ, but the setæ are longer and much more numerous than in the earthworm, and are borne on movable limbs or *parapodia*, of which a pair is

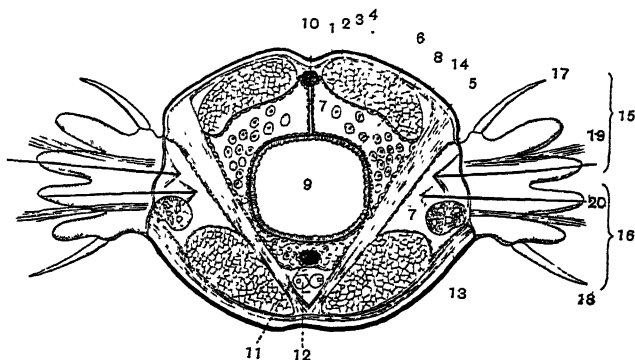


FIG. 127.—A transverse section through *Nereis cultrifer*, slightly simplified. The parapodia are shown in perspective. Magnified.
—From Shipley and MacBride.

- 1, Cuticle; 2, epidermis; 3, circular muscles; 4, longitudinal muscles; 5, oblique muscles forming a partition; 6, somatic layer of peritoneal epithelium; 7, cœlom; 8, splanchnic layer of epithelium; 9, cavity of intestine; 10, dorsal blood vessel; 11, ventral blood vessel; 12, ventral nerve cord; 13, nephridium in section; 14, ova; 15, notopodium; 16, neuropodium; 17, dorsal cirrus; 18, ventral cirrus; 19, setæ; 20, aciculus with muscles at inner end.

placed on each segment. A parapodium is a flat, hollow, vertical process of the body-wall, standing out at the side of its segment and serving to pull the animal along in creeping, or to row it in swimming. It is cleft into two principal lobes, a dorsal *notopodium* and a ventral *neuropodium*. Each of these is again divided into smaller lobes and bears at its base a slender process known as a *cirrus*. A stout, deeply embedded seta or *aciculus* supports the notopodium and another the neuropodium. The front end

of the body is modified to form a definite head. This consists of the prostomium and the peristomium. On the prostomium are situated dorsally a pair of *prostomial tentacles* and two pairs of eyes, each of which is a pit lined by pigmented cells and enclosing a gelatinous mass which serves as a lens. Ventrally the prostomium bears a pair of stout *palps*. The peristomium carries on each side two pairs of long, slender *tentacular cirri*, and probably corresponds to two fused segments. A bilaterally symmetrical animal which leads an active life always has a head, and if the animal be segmented there is a tendency

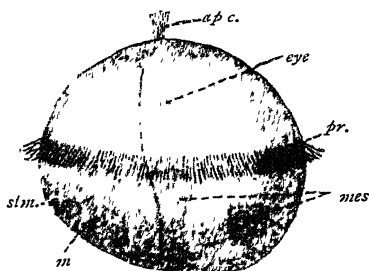


FIG. 128.—The trochosphere of *Nereis*.

—Modified, after Wilson.

ap.c., Apical tuft of cilia; *eye*, opening of mouth; *mes*, mesoderm; *pr.*, preoral ring of cilia; *st.m.*, stomodæum (the pouch of ectoderm which forms the mouth and gullet)

for the foremost segments to enter into the composition of the head. This is known as *cephalisation*. Behind the last segment is a conical region without parapodia which bears a pair of slender *anal cirri* and the terminal anus. The alimentary canal of *Nereis* is simpler than that of the earthworm, but the pharynx can be caused to protrude

by being turned inside out, and is lined with cuticle, thickened in places to form numerous small teeth and a pair of strong jaws with which the prey is seized. The sexes are separate. The reproductive organs are very simple, consisting of temporary masses of cells, which arise from the coelomic epithelium. The ova and sperm probably escape by temporary openings formed in the body-wall, and fertilisation takes place in the water. The free young are at first very unlike the parents, being minute, globular creatures, known as *trochospheres*, which swim by means of a girdle of cilia in front of the mouth and have an apical tuft at the front end. They

undergo a gradual change into the adult, becoming oval and then lengthening and segmenting.

Segmented, coelomate animals, with a thin cuticle, a closed blood-vascular system, and nephridia and a nervous system like those of the earthworm, are known as *Annelida*. The earthworm, *Nereis*, the lugworm (*Arenicola*), often used for bait, and leeches belong to this group.

CHAPTER XIV

THE CRAYFISH

CRAYFISHES are found in many English rivers, especially in those which rise in chalk or limestone hills.

Habits. They are little, lobster-like creatures, which make burrows in the river banks. They dislike strong light and during the daytime generally remain in their holes with only their pincers and long feelers projecting. When they come out they crawl stealthily about, searching constantly for their food, which consists of organic matter of any kind, plant or animal, dead or alive, that they are able to seize and break up with their pincers. If danger threatens, they dart backward suddenly and swiftly. They are used for food, especially for garnishing salads, and were formerly caught in large numbers in this country by means of crayfish-pots, but in 1887 their numbers were greatly reduced by a disease, and at present crayfishes for the table are imported from the Continent.

The English crayfish, *Astacus torrentium*, is about three inches long, and of a dull, greenish colour, which harmonises well with the surroundings in which it lives. The species imported from the Continent is *A. fluviatilis*, which is larger and has red colouring on the pincers and legs. The body of a crayfish is covered with a cuticle thickened and strengthened by salts of lime to form an armour: it is segmented, each segment bearing a pair of jointed limbs, but in the front part the segments are fused to form a *fore-body or cephalothorax*, where the only conspicuous sign of their existence is the presence of several pairs of limbs, though careful examination shows that parts of the armour and certain internal organs are also segmentally arranged. The rest of the

body, known as the *hind body or abdomen*, is more completely segmented. At the end of the abdomen is a flat piece known as the *telson*, on the under side of which the anus opens. The telson bears no limbs, and is divided by an imperfect transverse joint. The armour of each segment of the abdomen consists of a broad back-piece or *tergum* and a narrow belly-plate or *sternum*, with a pair of V-shaped prolongations, known as the *pleura*, joining them at the sides. There are no pleura on the first abdominal segment. The tergum, sternum, and pleura of each segment form a continuous ring. The limbs are jointed to the hinder side of the sternum near its outer ends, and the part of the sternum between each limb and the adjoining pleura is sometimes called an *epimeron*. The terga overlap one another from before backwards and slide over one another as the abdomen is straightened and bent, the armour of each segment being joined to that of the next by thin cuticle, which allows of movement. In the cephalothorax the terga are fused to form a *shield or carapace*. This is prolonged in front into a beak-like *rostrum* and is crossed by a furrow, which is called the *cervical groove* because it is supposed to mark the separation of two regions known as the head and thorax. At each side of the body a fold of the carapace overhangs as a lean-to roof, the *gill cover or branchiostegite*, which encloses between itself and the side of the body a chamber in which the gills lie. Behind the cervical groove a *branchiocardiac groove* on each side marks off the branchiostegite from a median *cardiac region* which roofs the thorax. The cuticle of the

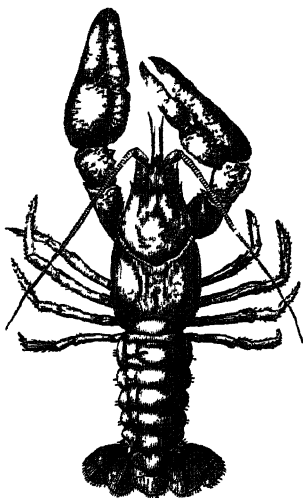


FIG 129 —View of a crayfish from above —After Huxley

Note cervical groove, cardiac region of carapace, rostrum, and tail fan

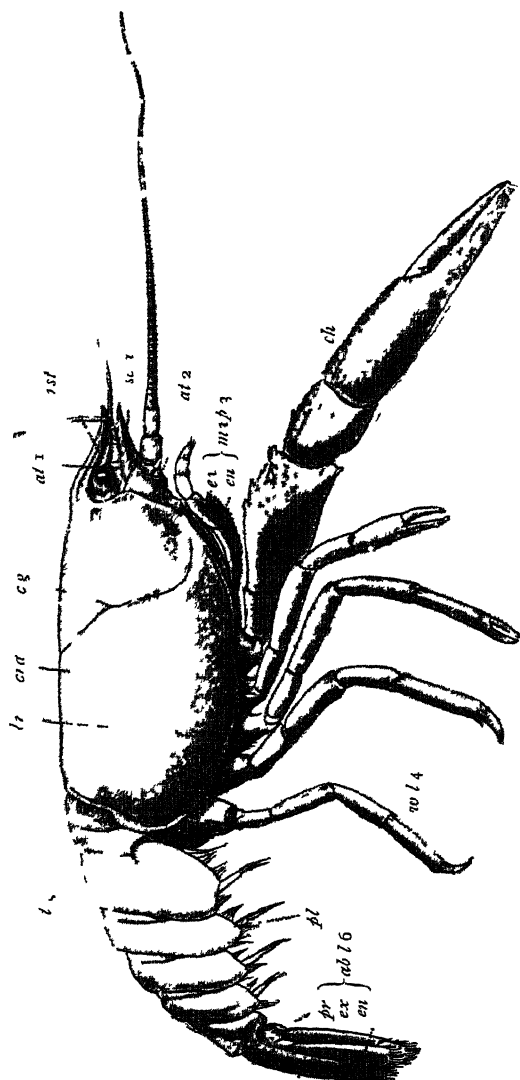


FIG 130 — View of a crayfish from the right side

ab 16, Sixth abdominal limb, *at 1*, antennule, *at 2*, antennar, *br*, branchiostegite, *cg*, cervical groove, *ch*, cheliped, *c1a*, cardiac region of carapace, *en*, endopodite, *ex*, exopodite, *m1p3*, third maxilliped, *pl*, pleon, *pr*, protopodite, *st*, rostrum, *sc 1*, scale of antennar, *t*, telson, *tg*, terga, *wl 4*, last walking leg

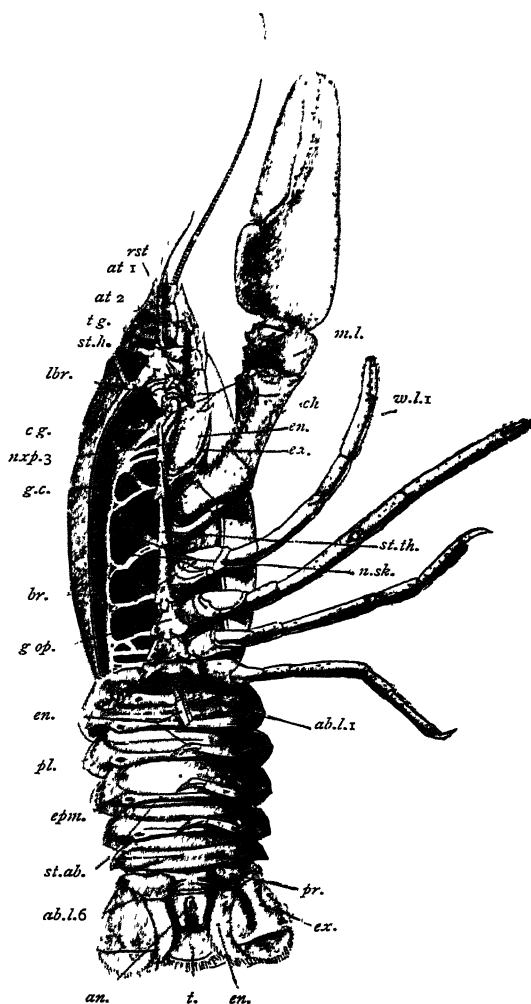


FIG. 131.—A ventral view of a female crayfish, with the limbs of the right side removed and the branchiostegite of that side partly cut away.—Partly after Howes.

ab.l.1,6, First and sixth abdominal limbs; *at.1,2*, antennae; *an.*, anus; *br.*, branchiostegite; *c.g.*, cervical groove; *ch.*, cheliped; *en.*, endopodite; *en.sk.*, endopodite; *epm.*, epimeron; *ex.*, exopodite; *g.c.*, gill chamber; *g.op.*, opening of oviduct; *lbr.*, labrum; *m.l.*, limbs adjoining the mouth; *nxp.3*, third maxilliped; *pl.*, pleuron; *pr.*, proto-podite; *rst.*, rostrum; *st.ab.*, abdominal sterna; *st.h.*, sternal region of body in part of mouth; *st.th.*, thoracic sterna; *t.*, telson; *tg.*, tubercle on which green gland opens; *wl.1*, first walking leg.

inside of the branchiostegite and part of the side of the body are thin. On the ventral side of the cephalothorax the limbs of each pair are close together, but small sterna lie between them. The head is, of course, the region which contains the mouth and the principal sense organs. The mouth is placed on the ventral surface at some distance from the front end, and in front of it the sternal surface slopes upwards to the rostrum. At the sides of the latter, upon a pair of short, movable stalks, are placed the eyes, and below these stand two pairs of feelers or antennæ.

The *limbs or appendages* number nineteen pairs, without counting the eyes, which are by some authorities reckoned as limbs. We shall not take this view, but as there is evidence in the development of the crayfish and of related animals that the foremost region of the head corresponds to a segment, we shall regard the body as containing twenty segments, of which the foremost bears no limbs. The telson is not a segment. Of the twenty segments, the first six form the head, the next eight the thorax, and the last six, with the telson, the abdomen. The parts of which a complete limb consists are best seen in the limbs known as the third pair of maxillipeds (Fig. 132, A), which lie immediately in front of the great pincers. In each of these we may distinguish a two-jointed basal region or *protopodite*, the joint nearest the body being known as the *coxopodite*, the next as the *basipodite*. On its outer side the coxopodite bears a large, flat, thin-walled structure known as the *epipodite*, covered with small finger processes, which constitute a *gill*. At the base of the epipodite is a knob bearing a tuft of threads known as the *coxopoditic setæ* or *setobranch*. The basipodite bears two structures. From its outer side arises a slender, jointed appendage known as the *exopodite*. At its end, continuing the axis of the limb, is the stout, five-jointed *endopodite*, whose joints, starting from the basipodite, are known as the *ischiopodite*, *meropodite*, *carpopodite*, *propodite*, and *dactylopodite*. The other limbs are built upon the same general plan as the third maxilliped, but in detail the structure of every one of them is adapted to the particular work it has to perform, each part being of a different shape in each pair of limbs, or sometimes

absent altogether. The first two pairs are sensory, and have long lashes for searching the surroundings of the animal. The next six pairs are jaws, used for bringing the food to the mouth and chewing it; these are short and stand close behind the mouth. Then come two great shears or pincers which are the principal grasping organs, next four pairs of legs, and then the six pairs of limbs of the abdomen, of which some are concerned in reproduction, some help the animal forward by paddling while it is walking, and the last pair are used in rapid swimming. Exopodites are wanting from the legs, great pincers, and first two pairs of jaws, and epipodites are found only upon the limbs of the thorax.

The first limb of each side is known as the *antennule* or *first antenna*. It is peculiar in having three, instead of two, joints in its protopodite. The first joint¹ is large and three sided; upon its upper side there opens, by a slit edged with bristles, the statocyst, which will be described later. The third joint bears two many jointed lashes or flagella. These are often compared to the exopodites and endopodites of the other limbs, but it is not certain that the comparison is justifiable. The outer lash bears on the under side of most of its joints certain peculiar bristles which are supposed to serve the sense of smell. The second limb is the *antenna* (or *second antenna*). Its coxopodite is short and wide and bears below a knob, upon which opens the green gland or kidney. The basipodite is divided lengthwise into two pieces. The exopodite is a flat, triangular, pointed *scale*, and the endopodite is a very long flagellum. The third limb or *mandible* has a large, broad, and very strong coxopodite² with a toothed edge which bites against that of its fellow on the other side of the body. The basipodite and an endopodite of two joints form a small three jointed appendage or *palp* in front of the

¹ See the following note.

² Perhaps really a joint known as the *precocxa*, which corresponds to the first joint of the antennule and is in the maxillule fused with the coxopodite. There is reason to believe that the so called coxopodite of the mandible is a *precocxa*, the true coxopodite being absent. In the second maxilla the *precocxa* may be represented by the first double lobe of the protopodite, and in the thorax the *precocxa* of each limb is absorbed into the side of the body. There is no evidence as to its identity in the abdominal limbs.

coxopodite. The mandibles lie at the sides of the mouth. Behind it come the limbs of the fourth pair, known as the *maxillules* or *first maxillæ*. Each of these consists of three thin plates joined to a small basal piece. One plate is an expansion of the coxopodite,¹ the second represents the basipodite, and the third the endopodite. The fifth limb is the *maxilla* (or *second maxilla*). It is a flat

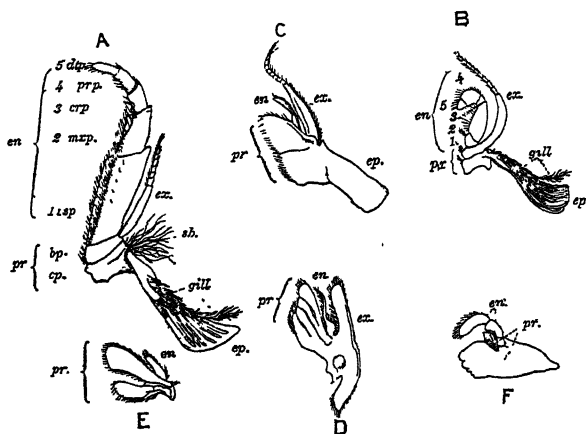


FIG. 132.—The mouth appendages of the left side of a crayfish.

A, Third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla (second maxilla); E, maxillule (first maxilla); F, mandible.
bb., Basipodite; *cp.*, coxopodite; *crp.*, carpopodite; *dtp.*, dactylopodite; *en.*, endopodite; *ep.*, epipodite; *ex.*, exopodite; *gill*, gill; *isp.*, ischiopodite; *mnp.*, meropodite; *pr.*, protopodite; *prp.*, propodite; *sb.*, setobranth or tuft of coxopoditic setae; 1-5, joints of endopodite.

structure, deeply cleft into several parts. The protopodite bears two thin lobes directed towards the middle line of the body and each in turn divided into two.² The endopodite is a narrow structure directed forwards. The exopodite is a wide plate projecting backwards and forwards from the outer side of the limb and known as the *scaphognathite*. The second maxilla lies within the front end of the

¹ See note 2 to p. 211.

² The first double lobe probably represents the precoxa; the two parts of the second lobe probably belong to the coxopodite and basipodite respectively.

branchiostegite, and the function of the scaphognathite is to set up a current of water over the gills by baling it forwards out of the gill chamber. The sixth limb, or *first maxilliped*, is the first of those which belong to the thorax. Two broad lobes represent its coxopodite and basipodite, the endopodite is small and two-jointed, and the exopodite, shaped like that of the third maxilliped, is large. The epipodite is present as a very large plate, which does not bear a gill. The *second maxilliped* is much like the third, but has a smaller endopodite and a relatively larger exopodite. The *third maxilliped* has already been described. Behind the maxillipeds come five pairs of *legs* or *pereiopoda*, of which the first, the ninth of the whole series

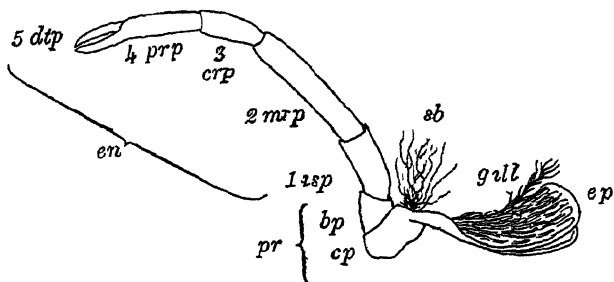


FIG 133 —The first walking leg of a crayfish. Letters as in Fig 132

of limbs, bear great pincers and are called the *chelipeds*, the rest being the *walking legs*. In each of these limbs the exopodite is wanting and the endopodite is long and strong and consists of five joints, named as in the third maxilliped. In the chelipeds and the walking legs of the first two pairs the last joint but one has a projection, against which the last joint bites so as to form a pair of pincers. An epipodite bearing a gill is present upon each of the legs except the last pair. On the coxopodite of the second walking leg of the female is a round opening, through which the eggs are laid, and the sperm of the male is passed through a similar opening upon the last leg. Of the *abdominal limbs* the first and second pairs are best studied after the third, fourth, and fifth. The latter are alike and consist

each of a short coxopodite, a long basipodite, and an endopodite and exopodite each composed of a number of imperfectly separated joints, of which the first is longer than the rest. The endopodite is rather longer than the exopodite, and both bear numerous plumed bristles. The *second abdominal limb* of the female is like those behind it. In the male the first joint of the endopodite is much elongated and bears at the end on the outside a thin plate rolled into a scroll. The *first abdominal limb* has no exopodite in either sex. In the female it is minute. In the male the basipodite and endopodite are fused, flattened, and rolled scrollwise into a tube for conveying sperm to the female. The limbs of the *last (sixth) abdominal pair* have short, undivided protopodites, and very broad endopodites and exopodites, the former of one, the latter of two joints. They are directed backwards, and form with the telson the *tail fan* used in swimming.

Table of the Segments of the Crayfish

	1. Preantennal limbless segment.	
Head .	2. Antennules	} Sensory limbs.
	3. Antennæ (II)	
	4. Mandibles	
	5. Maxillules	} Jaws.
	6. Maxillæ (II)	
	7. Maxillipeds (I)	
Thorax .	8. " (II)	} Legs.
	9. " (III)	
	10. Chelipeds	
	11. Walking legs (I)	
	12. " " (II) ♀	
	13. " " (III)	
Abdomen	14. " " (IV) ♂	} Uniramous limbs.
	15. Abdominal limbs (I)	
	16. " " (II)	
	17. " " (III)	} Paddles.
	18. " " (IV)	
	19. " " (V)	
	20. " " (VI)	} Tail fan.
	Telson	
♀ Female opening.		♂ Male opening.

The ectoderm or epidermis of the crayfish consists of a layer of protoplasm with nuclei, which in many parts is not

divided into cells and is therefore a syncytium (p. 116), though in places it forms a columnar epithelium. Outside it lies a cuticle which it secretes, and, as we have already seen, this cuticle is for the most part thick and hardened with salts of lime, so as to form an armour, but remains thin and flexible in certain places so as to form joints which allow the parts of the body to move upon one another, and also in the gill chambers. In many places it bears bristles of various shapes. These are hollow, and the epidermis is continued into them and is here often connected with nerve fibres, so that the bristles serve as sense organs of various kinds. From time to time the cuticle is shed and a new one secreted. This allows of growth and also serves as a form of excretion, for the horny basis of the cuticle, known as *chitin*, is a complex compound of ammonia, so that in it the animal gets rid of nitrogenous waste matter. Moulting takes place frequently while the animal is growing, but the full-grown male sheds its cuticle only twice a year, and the female only once. As the time for moulting draws near, the crayfish goes into hiding, because the new cuticle is soft and the animal will be helpless for some days while it is hardening. The shell then splits across the back and along the limbs, and the crayfish, lying on its side, draws itself out of the old cuticle.

There is in the crayfish no continuous muscular body-wall, but numerous muscles, composed of striped fibres, move the various parts of its body, being attached to the inside of the pieces of the armour.

Thus the skeleton is external, not, like that of a frog, internal. In the thorax ingrowths of the cuticle provide a kind of false internal skeleton. This has the form of a complicated scaffolding along the ventral side of the animal, and is known as the *endophragmal skeleton*. Two very powerful sets of muscles move the abdomen. A dorsal set of *extensor muscles* starts from the inside of the carapace and is inserted into the terga of the abdominal segments. When they contract, these muscles draw forward the terga and thus straighten the abdomen. On the ventral side another set of muscles connects the sterna with one another and with the endophragmal skeleton. These, when

they contract, draw closer the sterna and thus bend the abdomen. By these movements, spreading at the same time its tail fan, the crayfish carries out the sudden backward jumps by which it escapes from its enemies. Its gentle forward movements are carried out by the walking legs, aided by a paddling of the abdominal limbs. The legs of the first three pairs pull and those of the last pair push, and their movements are carried out in such a

way that the animal is always standing upon six legs while two—which are on opposite sides and of different pairs—are in motion.

The body of the crayfish contains a spacious perivisceral cavity, in which the internal organs lie. This is not a coelom, but an enlarged portion of the hæmocœle (p. 201), and communicates with the blood vessels. The alimentary canal fills the greater part of this cavity. The

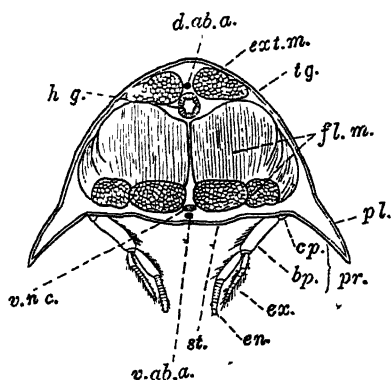


FIG. 134.—A semi-diagrammatic drawing of a transverse section of the abdomen of the crayfish.

bp., Basipodite; *cp.*, coxopodite; *d.ab.a.*, dorsal abdominal artery; *en.*, endopodite; *ex.*, exopodite; *ext.m.*, extensor muscles; *fl.m.*, flexor muscles; *h.g.*, hind-gut; *pl.*, pleuron; *pr.*, protopodite; *tg.*, tergum; *st.*, sternum; *v.ab.a.*, ventral abdominal artery; *v.n.c.*, ventral nerve cord.

mouth is an elongated opening below the head between the mandibles. It is bordered in front by a wide *upper lip or labrum*, and behind it stands a pair of lobes known together as the *lower lip or metastoma*. A short, wide *gullet* leads upwards into the large *proventriculus*, often called the "stomach." This consists of two chambers, a large *forepart or mill-chamber*, often known as the "cardiac division of the stomach," and a smaller *hind part or filter-chamber*, often known as the "pyloric division of

the stomach," separated from the mill-chamber by a pit in the roof. From the filter-chamber the short *mid-gut*

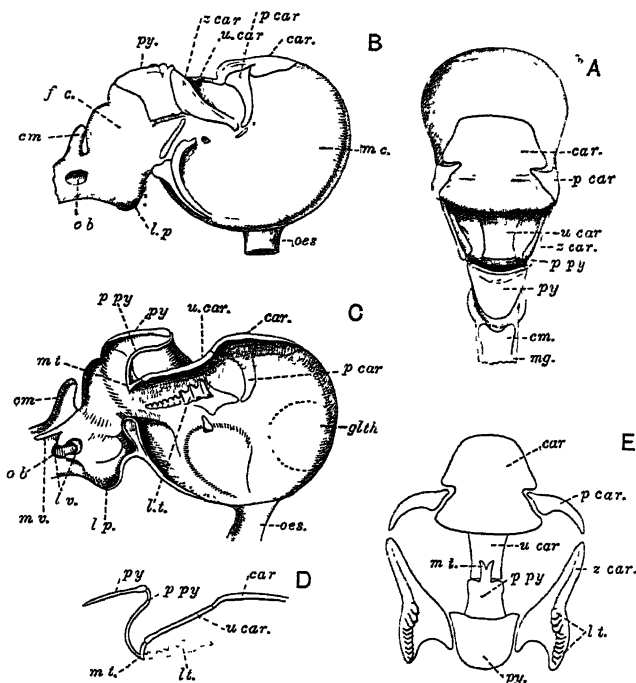


FIG. 135.—The proventriculus of the crayfish.

A, The whole organ from above; *B*, the same from the right side; *C*, the left half from within, the muscles being relaxed; *D*, the ossicles of the mill in median section, the anterior and posterior gastric muscles being contracted; *E*, the mill in plan. All the figures are semi-diagrammatic, much detail being omitted.

car., Cardiac ossicle; *cm.*, cœcum; *f. c.*, pyloric or filter-chamber; *glth.*, position of gastrolith; *l. p.*, lateral pouch; *l. t.*, lateral tooth; *l. v.*, lateral valves guarding opening into mesenteron; *m. c.*, mill-chamber; *m. t.*, median tooth; *m. v.*, median valve; *o. b.*, opening of bile duct; *oes.*, œsophagus; *p. car.*, pterocardiac ossicle; *p. py.*, prepyloric ossicle; *py.*, pyloric ossicle; *u. car.*, urocardiac ossicle; *z. car.*, zygocardiac ossicle.

or mesenteron leads backwards to the long *hind-gut*, sometimes called the "intestine." The epidermis and cuticle turn inwards at the mouth and line the gullet and pro-

ventriculus, which are together known as the *fore-gut*. The mid-gut is lined with soft endoderm, and the hind-gut is again lined with epidermis and cuticle. Thus the regions often called stomach and intestine in the crayfish do not correspond with those so named in the frog and earthworm, being lined with ectoderm, not endoderm. The cuticle in the gut is for the most part thin, but in places in the proventriculus it forms stout plates or ossicles, certain of which bear strong teeth which project into the forepart of the organ. By the action of muscles these can be brought together to crush the food. The whole apparatus is known as the *gastric mill*.

Two large plates lie across the roof in the two divisions, and are known as the *cardiac* and *pyloric ossicles*. They are joined in the middle by two smaller pieces, the *urocardiac* and *prepyloric ossicles*, which lie respectively in the front and hinder walls of the pit between the two divisions. From the lower end of the prepyloric ossicle there projects into the proventriculus the forked *middle tooth*. When the mill is at rest the pit passes backwards, so that the prepyloric ossicle in its hinder wall is also directed backwards under the pyloric and its tooth points backwards. At each side of the pit the cardiac and pyloric ossicles are connected by two more pieces, the *zygocardiac ossicle*, which articulates behind with the side of the pyloric, and the *pterocardiac ossicle*, which joins the front end of the zygocardiac to the side of the cardiac ossicle. These side ossicles do not run straight, but slope outwards to meet at an angle, so that the outline of the whole framework of the mill is roughly hexagonal. Internally each zygocardiac ossicle bears a large, ribbed, *lateral tooth*. *Anterior* and *posterior gastric muscles* run from the cardiac and pyloric ossicles respectively to the carapace. When they contract they pull these ossicles apart. The result is that (1) the upper end of the prepyloric ossicle, being pulled backward by the pyloric, stands upright, thus turning the middle tooth forwards; (2) the zygocardiac and pterocardiac ossicles are straightened out, so that the lateral teeth are brought together in the middle line. Thus all three teeth meet inside the proventriculus.

The filter-chamber is also complicated, having various internal ridges covered with bristles which serve to strain out the particles of the food, so that only the finely crushed matter passes into the mid-gut. Into this opens on each side the *liver or hepatopancreas*, a large, lobed, yellow gland, consisting of numerous short tubes joined by ducts which finally communicate with the mid-gut by an opening on each side. The roof of the mid-gut is prolonged into

a short *blind gut* or *cæcum*. Food is either raked up by the third maxillipeds or seized by the chelipeds and torn up by them and the smaller pincers. It is passed forwards by the jaws to the mouth, where it is cut up by the mandibles into pieces small enough to be swallowed. These are chewed in the proventriculus, strained and in a finely divided state passed into the mid-gut. The juice secreted by the liver digests all classes of food stuffs, and digestion and absorption take place within the liver as well as in the mid gut. The cuticle of the gut is shed with that of the body. Shortly before a moult two flat calcareous bodies, known as "*crab's eyes*" or *gastroliths*, are laid down in the forepart of the proventriculus. They are ground up before the moult takes place. It is uncertain whether they consist of matter removed from the armour of the body to weaken it in preparation for the moult or are a store of material for the strengthening of the new cuticle. Possibly they serve both purposes.

The heart is a hollow organ with thick, muscular walls.

Blood Vessels It is roughly hexagonal in outline, as seen from above, and lies in the thorax, above the hind gut and immediately below the cardiac region of the carapace, in a space, known as the *pericardial sinus*, with membranous walls, to which the heart is connected by six fibrous bands called the *alæ cordis*. Three pairs of valved openings or *ostia* admit blood from the pericardial sinus to the heart: one pair is dorsal, another lateral, and the third ventral. From the front end of the heart arise three vessels—a median *ophthalmic artery*, which runs straight forwards over the proventriculus to supply the eyes and other organs of the head, and a pair of *antennary arteries*, which start one on each side of the ophthalmic, run forwards and outwards, and divide each into two branches, one *gastric* and the other to the antennæ and green gland. Behind and below the antennaries arises a pair of *hepatic arteries*, which supply the liver, and from the hinder angle of the heart there is given off a vessel which at once divides into a *dorsal abdominal artery*, which runs backwards above the intestine and supplies it and the muscles of the abdomen, and a *sternal artery*. This passes downwards, through an opening in the ventral nerve cord, and divides

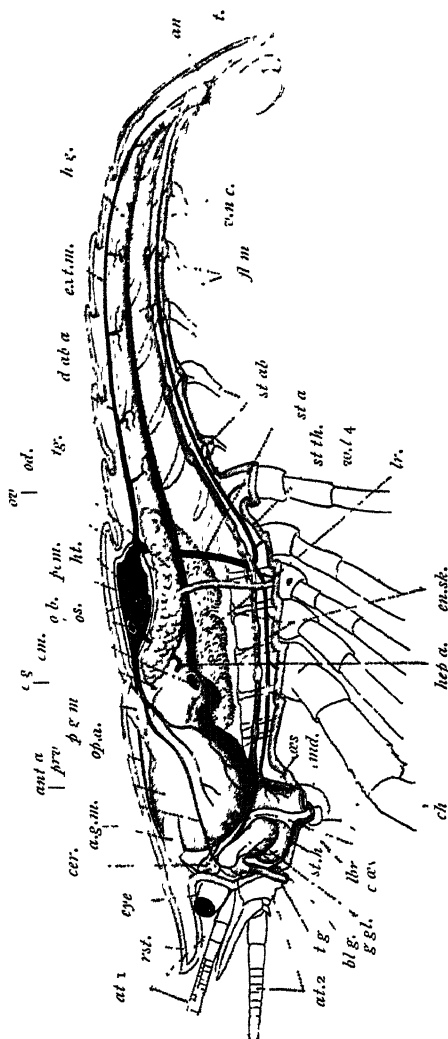


FIG. 136.—A female crayfish dissected from the left side.—Partly after Shipley and MacBride.

a.g.m., Anterior gastric muscle; *an.*, anus; *ant.a.*, antennary artery; *at.1*, antennule; *at.2*, antenna; *bl.g.*, bladder of the green gland; *c.g.*, cervical groove; *c.œs.*, circumoesophageal commissure; *cer.*, cerebral ganglion; *ch.*, cheliped, *cm.*, cæcum, *d.ab.a.*, dorsal abdominal artery; *en.sk.*, endophragmal skeleton; *eye*, *ext.m.*, extensor muscles; *fl.m.*, flexor muscles; *g.g.*, green gland; *h.g.*, hind-gut; *hep.a.*, hepatic artery; *ht.*, heart; *l.*, liver; *lb.*, labrum; *md.*, mandible; *m.p.*, mandibular palp; *o.b.*, opening of bile duct; *od.*, oviduct; *œs.*, oesophagus, *op.a.*, ophthalmic artery; *os.*, ostia; *ov.*, ovary; *p.g.m.*, posterior gastric muscle; *pen.*, pericardium; *prv.*, proventriculus; *rst.*, rostrum; *st.a.*, sternal artery, *st.ab.*, abdominal sterna; *st.h.*, sternal region of the body in front of the mouth, *st.th.*, thoracic sterna; *t.*, telson; *t.g.*, terga; *v.h.c.*, ventral nerve cord; *w.l.4*, last walking leg.

into a *ventral abdominal* and a *ventral thoracic* artery, by which the limbs are supplied. Each of the arteries branches many times, till it finally gives rise to minute vessels in the organs it supplies, but there are no capillaries. The blood from the organs passes into great *sinuses* which

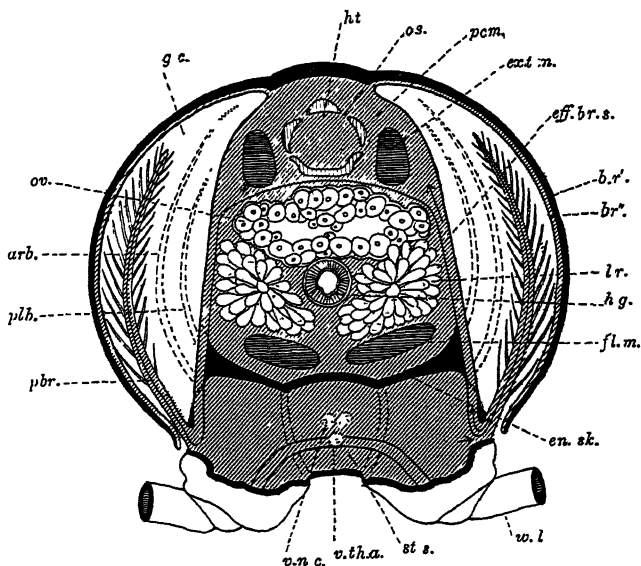


FIG. 137.—A diagram of a transverse section through the thorax of a crayfish.

arb., Arthrobranch; *br'*, outer layer of branchiostegite; *br''*, inner layer of the same; *eff.br.s.*, efferent branchial sinus; *en.sk.*, endophragmal skeleton; *ext.m.*, extensor muscle of abdomen; *fl.m.*, flexor muscles of abdomen; *g.c.*, gill-chamber; *h.g.*, hind-gut; *ht*, heart; *br.*, liver; *os*, ostia; *ov.*, ovary; *pcm.*, pericardium; *pbr.*, podobranch; *plb.*, pleurobranch; *st.s.*, sternal sinus; *v.n.c.*, ventral nerve cord; *v.th.a.*, ventral thoracic artery; *w.l.*, walking leg.

surround them. The largest of these is the perivisceral cavity, but there are also blood spaces in the limbs and elsewhere. The blood from the limbs and a great part of that from the perivisceral cavity is gathered up into a *sternal sinus*, which lies in a tunnel formed by the endophragmal skeleton and contains the ventral nerve cord

and ventral thoracic artery. From this a series of *afferent branchial sinuses* carries the blood to the gills, where it is oxygenated. From the gills it passes by *efferent branchial sinuses* to the pericardial sinus. Part of the blood from around the stomach, however, passes into the space between the two sides of the fold of carapace which forms the branchiostegite, and thence to the pericardial sinus by a vessel which follows the hinder edge of the branchiostegite. It will be noted that the pericardial cavity of the crayfish

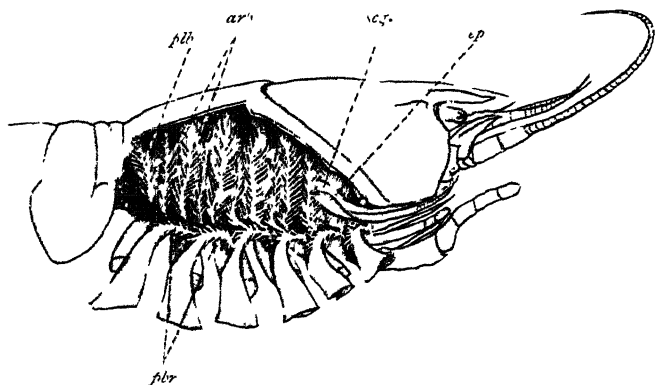


FIG. 138.—The forepart of the body of a crayfish, viewed from the right-hand side, with the legs and the branchiostegite cut away and the gills displayed.

arb., Arthrobranchia; *ep*, epipodite of the first maxilliped; *pbr.*, podobranchia; *plb.*, pleurobranchia; *scg.*, scaphognathite.

is a part of the hæmocœle and contains blood, unlike that of the frog, which is a separate part of the coelom. A blood-vascular system in which, as in the crayfish, the blood on leaving the arteries bathes the organs of the body is said to be *open*. One in which, as in the worm and the frog, it is carried through the organs in capillaries which lead direct to veins is said to be *closed*. The blood is a clear fluid which clots readily and contains white corpuscles. An organic compound of copper, known as *hæmocyanin*, which is dissolved in it, plays the same part as hæmoglobin, taking up oxygen in the respiratory organs

and parting with it to the tissues. In the oxidised condition it is of a blue colour and tinges the blood.

The respiratory apparatus of the crayfish is contained in the gill-chambers. The *gills* are branched, thin-walled structures, standing upon the coxopodites of the thoracic limbs and the inner wall of the gill-chamber. In them the blood circulates and exchanges its carbon dioxide for the oxygen which is dissolved in the water that is kept flowing through the chamber by the action of the second maxilla. This limb is held firm by the curved end of its endopodite, which fits into a groove upon the mandible at the base of the palp, while the exopodite or scaphognathite, flapping at the rate of sixty strokes a minute, bales water forwards, out of the gill-chamber and under the opening upon the antenna of the green gland, whose excreta it thus sweeps away with the foul water from the gills. By this action fresh water is drawn into the chamber between the bases of the legs. No doubt the blood in the branchiostegite is oxygenated through the thin inner wall of that organ.

The gills receive different names according to their position. Those which are attached to the epipodites of the limbs are known as *podobranchiæ*. Others stand upon the membranes which join the limbs to the body, and are known as *arthrobranchiæ*, and a few stand upon the inner wall of the gill-chamber (the side wall of the thorax) above the legs, and are known as *pleurobranchiæ*. A podobranchia is found on every thoracic limb, except the first pair of maxillipeds, which have no gills,¹ and the last pair of legs, which have only a pleurobranchia. Two arthrobranchiæ, an anterior and a posterior, are found upon each limb that has a podobranchia, except the second maxilliped,

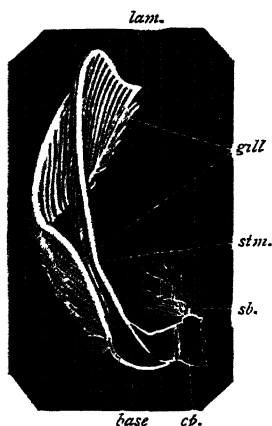


FIG. 139.—A podobranch of the crayfish, seen from behind.

Base; *cp.*, coxopodite; *gill*; *lam.*, lamina; *sb.*, setobranch or tuft of coxopoditic setæ; *stm.*, stem.

¹ In *A. fluviatilis* they have each a vestigial arthrobranchia.

which has only the anterior arthribranchia. Well-developed pleurobranchiæ are only found above the legs of the last pair, but in the same position above each leg of the three preceding pairs there is a minute process which represents a gill. The following table shows the position of the gills:—

	Maxillipeds.				Legs.				Total.
	1	2	3	1	2	3	4	5	
Podobranchiæ .	Ep	1	1	1	1	1	1	0	6 + Ep
Anterior arthrobranchiæ .	0	1	1	1	1	1	1	0	6 } 11
Posterior arthrobranchiæ .	0	0	1	1	1	1	1	0	
Pleurobranchiæ	0	0	0	0	R	R	R	1	1 + 3R
Total .	Ep	2	3	3	3 + R	3 + R	3 + R	1	18 + 3R + Ep

Ep = epipodite without a gill.

R = abortive rudiment.

Each arthrobranchia has a tree-like structure, consisting of a trunk or *axis* arising from the body by one end, with numerous short branches or *filaments*. The two pleurobranchiæ have the same structure. In the podobranchiæ the axis is fused to the epipodite along the greater part of its length, so that the filaments appear to arise from the epipodite. The tip of the gill, however, stands free. The epipodite itself is a long plate with a wide *base*, a narrower *stem*, and at the end a second expansion, the *lamina*. The stem and lamina are folded along the length of the epipodite, so that a groove is formed, into which fits the gill of the limb next behind.

The excretory organs of the crayfish are known as the *green glands*. They lie in the head immediately behind the antennæ, upon whose basal joints their ducts open. The duct is connected with a thin-walled bladder, below which lies a green mass. This has a complicated structure, which may be summed up by saying that it is a labyrinth of spaces whose walls are lined by a cubical, glandular epithelium differing in character in different regions. In the middle of it is a small, brownish sac whose cavity is divided by partitions and communicates by a single opening with the labyrinth. This

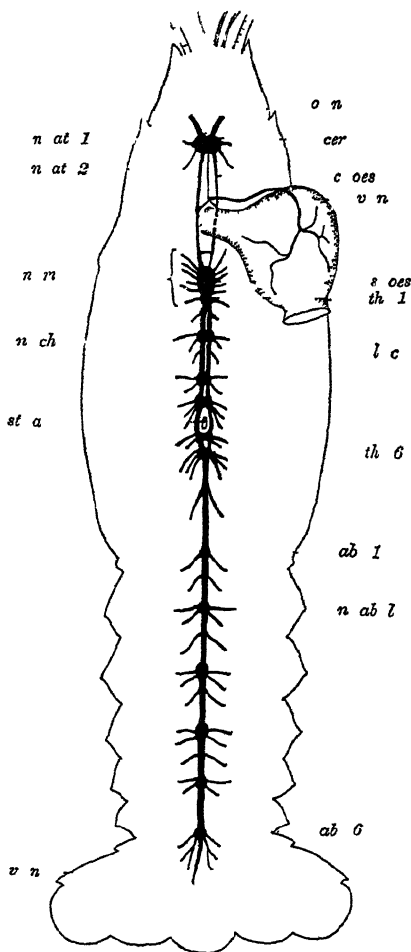
**Excretory
Organs.**

is known as the *end sac*. The labyrinth has been compared to a nephridium and the end sac regarded as a minute portion of the coelom, which is otherwise represented in the crayfish only by the cavity of the genital organ.

In its general plan the nervous system of the crayfish resembles that of the earth worm. In the front part of the head, between the green glands, lies a *supra-oesophageal or cerebral ganglion, or brain*, which corresponds in position to the supra-pharyngeal ganglia of the worm. It gives nerves to the eyes, antennules, and an

FIG. 140.—A semi diagrammatic view of central nervous system of a crayfish.

ab 1 *ab 6* The first and sixth abdominal ganglia. *cer*, cerebral ganglion. *c. oes*, circumoesophageal commissure. *l. c.*, longitudinal commissures of ventral cord. *n. abl*, nerves to abdominal limbs. *n. at 1*, nerve to antennule. *n. at 2*, nerve to antenna. *n. ch*, nerve to cheliped. *n. m*, nerves to limbs adjoining the mouth. *o. n.*, optic nerve. *s. oes*, suboesophageal ganglion. *st. a.*, sternal artery. *th 1*, *th 6*, first and sixth thoracic ganglia. *n. n.*, nerve to proven tricus. *v. n.*, nerve to hind gut.



tennæ, and from it two long *circumœsophageal commissures* pass backwards to join behind the œsophagus in the *sub-œsophageal ganglion*. This gives nerves to the limbs as far as the second maxillipeds inclusive, and immediately behind it lies the *first thoracic ganglion*, which supplies the third maxillipeds. In each of the remaining segments of the thorax lies an indistinctly double ganglion which supplies by several nerves the limbs and other organs of its segment. These ganglia are set at some distance apart and are connected by double commissures, forming thus a *ventral cord*. Between the fourth and fifth ganglia the commissures part widely to allow the sternal artery to pass between them. In the abdomen the cord is continued and consists of a ganglion in each segment united to its fellows by longitudinal commissures which are really double, but appear at first sight to be single. The last ganglion supplies the telson as well as its own segment.

A *transverse commissure* immediately behind the œsophagus joins the two circumœsophageal commissures. It contains fibres which take this roundabout course between the portions of the brain which supply the antennæ, thus indicating that these limbs belong to the same series as those behind the mouth. This is probably also true of the antennules, and the fact that the limbs of the first two segments are innervated from the supracœsophageal ganglia must be connected with the position of the mouth, which is further back than in the earthworm, where it lies in front of the first segment. The alimentary canal is supplied by two *visceral nerves*. The first has a threefold origin, being formed by the junction of a nerve from the cerebral ganglion with two nerves which arise each from a small ganglion on the course of the circumœsophageal commissure. The second arises from the last abdominal ganglion.

The eyes of the crayfish are *compound*, containing a number of elements, known as *ommatidia*, each of which is a small complete eye. The whole eye is black, owing to the presence of pigment in some of its cells, and is covered with a colourless portion of the cuticle known as the *cornea*, divided into a number of square facets, each of which corresponds to an ommatidium. The structure of the ommatidia is complex: each is an elongated body consisting of a number of cells derived from the epidermis with refractive bodies secreted by them. The innermost cells form a group known as the *retinula*, whose

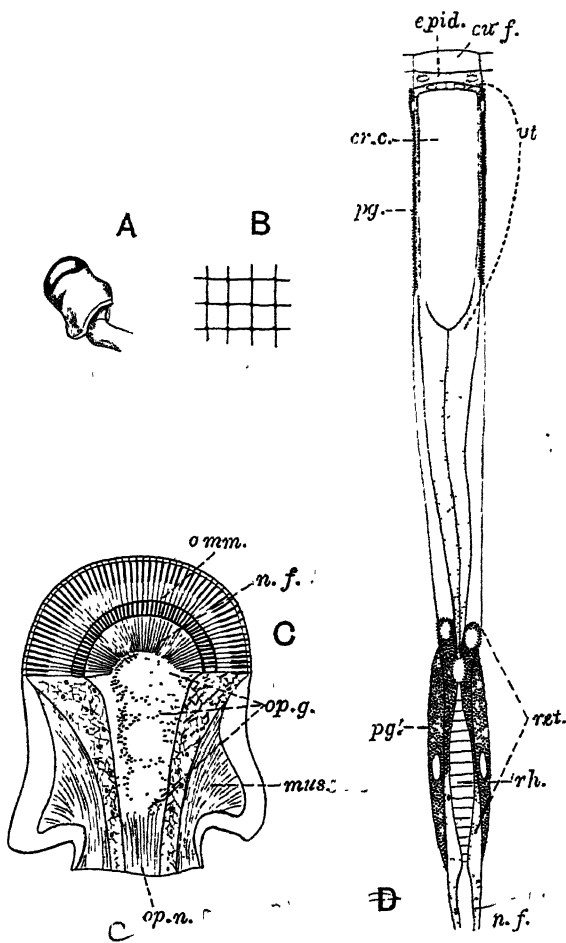


FIG. 141.—The eye of the crayfish. D

A, The left eye removed; B, a portion of the cornea magnified to show the facets; C, a longitudinal section of the eye under low magnification; D, a single ommatidium highly magnified.—D after Parker.

cr.c., Outer refractive body or crystalline cone; *cu.f.*, cuticular facet; *epid.*, epidermis (hypodermis); *mus.*, muscles which move the eye; *n.f.*, nerve fibres; *omm.*, ommatidia; *op.g.*, optic ganglion; *op.n.*, optic nerve; *p.g.*, outer pigment cells; *p.g.*, inner pigment cells; *ret.*, retinula cells (the sense cells)—these cells contain pigment; *rh.*, inner refractive body or rhabdome; *vt.*, vitellæ or cells which secrete the crystalline cone.

inner ends are continued into nerve fibres. The ommatidia are separated by pigment cells and the retinular cells also contain pigment. The way in which such eyes give rise to vision has been the subject of various theories. It appears

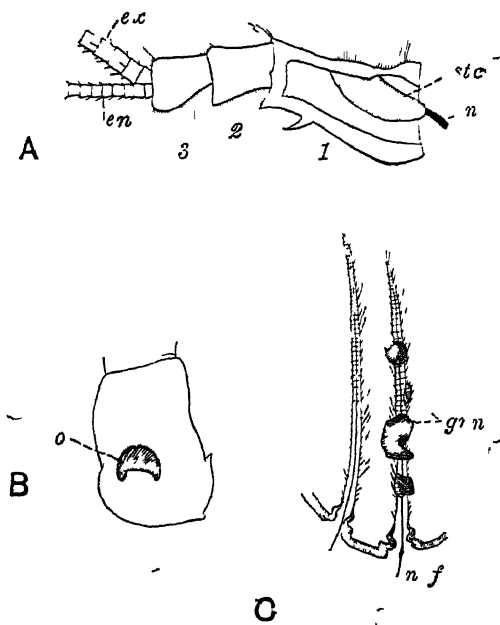


FIG. 142 —The statocyst of the crayfish

A The right antennule seen from the median side with the basal joint opened and the flagella cut short, *B*, basal joint of the left antennule from above *C*, two hairs from the statocyst —C partly after Howes

en Inner flagellum *ec* outer flagellum *gr* sand grains *n* nerve of the statocyst *nf* nerve fibres *o*, opening of the statocyst *sc* statocyst

that the pigment flows about within the cells, being retracted in weak light and expanded in strong. When it is retracted the eye gives a single image, when it is expanded each retinula gives a separate image, sharper but formed with a greater loss of light than that given when the eye acts as a

whole. No doubt this *mosaic* of images is combined in the nervous system to give a single impression.

The *statocysts* are a pair of sacs, situated in the basal joints of the antennules and provided with nerves. Each has a cuticular lining beset with hairs, with which the nerve fibres are in communication. Within it are grains of sand, which are scattered over the opening of the sac by the pincers and fall into it. It is probable that the principal function of the organ is informing the animal of its position by the movements of the sand grains against the hairs, and

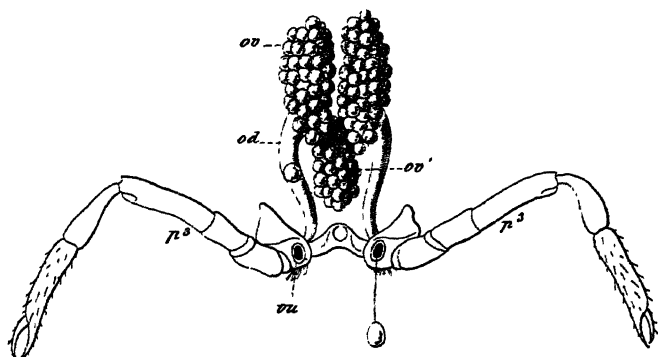


FIG. 143.—The reproductive organs of a female crayfish.—
After Suckow.

od., Oviduct; *ov.* ovaries; *ov'*, fused posterior part (median lobe);
vu, female aperture on the second walking leg (*p*²).

thus enabling it to keep its equilibrium. If the statocysts be removed, the crayfish loses its sense of position and will often swim upside down. Experiments upon the prawn, an animal related to the crayfish, illustrate the function of the statocysts. A prawn that had lost the lining of its statocysts with the sand grains by moulting was kept in filtered water and supplied with finely powdered iron in place of sand. When it had placed some of these in its statocysts, a magnet was brought near it, and by moving the magnet the particles of iron were caused to move as they would be by a change in the position of the animal. By this means the prawn was made to alter its position in

correspondence with the movements of the magnet. It was formerly supposed that the statocysts subserved the sense of *hearing*, but though the animals appear to perceive vibrations, and this may be due to the statocysts, it is doubtful whether the latter are true organs of hearing. We have seen that the antennules bear on their outer flagella bristles which subserve the sense of *smell*. Various of the setæ, especially those of the antennæ, are organs of *touch*.

The sexes of the crayfish are separate. The



FIG. 144. — The reproductive organs of a male crayfish.— After Huxley.

t., Testes; *vd.*, vas deferens; *vd'*, opening of vas deferens on last walking leg.

Reproduction. generative organs lie in the thorax, above the gut and below the pericardium. They have the same general shape in the two sexes, consisting of three lobes, two anterior and one posterior, with a pair of ducts, which start from the junction of the anterior and posterior lobes and run to the limbs on which they open. The ovary is larger and broader than the testis, and has an internal cavity into which the eggs are shed. The oviducts are short, straight, and wide; they open upon the coxopodites of the second pair of walking legs. The testes consist of a number of branching ducts which end in small alveoli,

in which the spermatozoa are formed. The vasa deferentia are narrow and much coiled; their first part is very slender and translucent, the second part, which forms most of the duct, is wider and glandular, and a short terminal region has muscular walls which force out the sperm. The *spermatozoa* are discs with stiff, pointed processes round the edge. Inside the disc is a round capsule and to one side of this a small, oval body. Pairing takes place in September and October. The male seizes the female,

throws her upon her back, and passes sperm through the tubular limbs of his first abdominal segment on to the parts in the neighbourhood of her oviducts, the limbs of his second abdominal pair aiding the process by working to and fro on the hollows of the first. The sperm consists

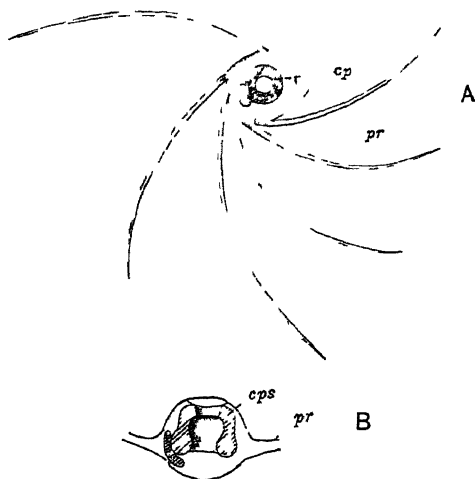


FIG 145 —Spermatozoa of a cray fish

A, Whole spermatozoon from above *B* part enlarged, from the side

cps, Capsule *pr*, stiff processes

of a sticky substance, secreted by the vasa deferentia, carrying the spermatozoa, and forms white masses on the sterna of the female. The eggs, which are large and yolky, are laid in November. The processes of the spermatozoa adhere to them, and by a sudden expansion of the capsule the rest of the body is forced into the ovum. Each egg is attached to one of the hairs on the abdominal limbs

by a stalked shell formed of a substance secreted by certain glands on the sterna, and is thus under the protection of the mother during its development. By the division of the nucleus of the fertilised ovum a syncytium is formed

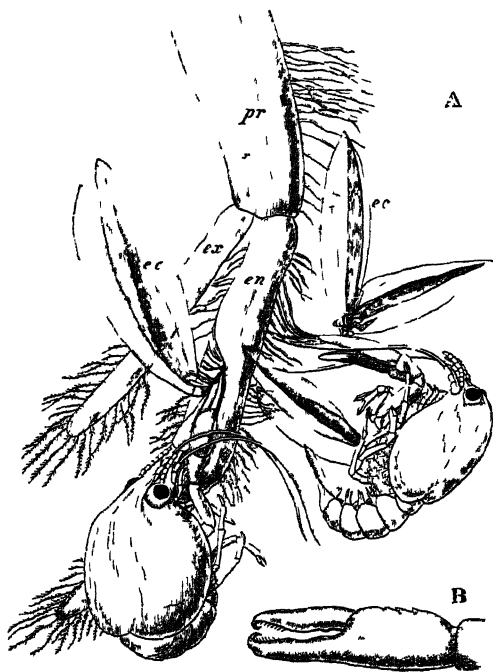


FIG. 146—*A*, two recently hatched crayfish holding on to one of the swimmerets of the mother, *B*, pincers of such crayfish more highly magnified.—From Huxley

ec Ruptured egg cases, *en*, endopodite *ex* exopodite *pr* protopodite

which does not divide into cells until a number of nuclei have arisen. The young are hatched at the beginning of the next summer. They do not differ greatly from the adult, but have curved tips to the pincers, by which they cling for a time to the empty shell or the abdominal

limbs of the mother, and are thus protected from enemies and kept from being swept away by currents and so eventually reaching the sea, where they would perish.

The power of regeneration, though it is less in the crayfish than in earthworms and much less than in *Hydra*, is still considerable. A whole limb which is injured can be grown again. The injured leg is first cast off by a spasmodic contraction of some of its muscles which causes it to break through at the basipodite, the internal cavity being here crossed by a partition which leaves only a small opening, through which the nerves and blood vessels pass. When the limb is cast off this opening is quickly closed by a blood clot, after which the cuticle grows across the wound. Beneath the scar the new limb is formed as a sort of bud and gradually takes shape. At the next moult it becomes free, though it is still small, and it increases in size at each moult until a normal limb has been provided. This power of casting off limbs is known as *autotomy*. It is sometimes used as a means of escape from enemies which have seized one of the limbs, but this is not so common in the crayfish as in some animals that are related to it.

Segmented animals with jointed limbs, a thick cuticle, an open blood-vascular system, and a nervous system like that of the crayfish are known as *Arthropoda*. Insects, spiders, and centipedes belong to this group.

CHAPTER XV

INSECTS

COMMON as they now are, cockroaches have only been introduced into England comparatively recently. **Cockroaches.** The first specimens were brought from the East by trading vessels at the beginning of the seventeenth century, and one hundred and fifty years later Gilbert White could still speak of the cockroach as "an unusual insect" at Selborne. This species was the Common Cockroach, *Periplaneta orientalis*. More recently another species, *P. americana*, a native of tropical America, has been introduced and is spreading rapidly. Both are nocturnal insects which haunt human dwellings, hiding in corners and crevices by day. They seek warmth, as is natural in view of their origin, and devour any kind of food they can find.

In its main lines the anatomy of a cockroach resembles that of a crayfish. The animal is segmented, **Anatomy of a Cockroach.** the segments being unlike and grouped into three regions known as head, thorax, and abdomen, but these do not correspond with the parts similarly named in the crayfish. There is a thick cuticle, and jointed limbs are found on the head and thorax. The thorax bears also two pairs of wings. At the sides of the head lie a pair of large, unstalked, compound eyes. The coelom, of which traces are found in development, disappears in the adult, but there is a hæmocoelic perivisceral cavity containing blood.

The head is short and deep. Seen from in front it has a pear-shaped outline, with the narrow end downwards. Its armour consists of several pieces—two *epicranial plates* side by side above, two *genæ* at the sides below the eyes, and a *clypeus* in front. A labrum

is hinged on to the clypeus below. The appendages of the head are as follows. There is one pair of long, slender, unbranched, many jointed antennæ, corresponding to the antennules of the crayfish. The second antennæ of the latter are not represented in the cockroach. The mandibles are stout, toothed structures without palps, not unlike the basal parts of those of the crayfish. The maxillules of the crayfish are not represented in the cockroach, though in certain primitive insects corresponding structures are present. The maxillæ consist of (a) a protopodite of two joints known as the *cardo* and *stipes*, (b) a five jointed exopodite known as the *maxillary palp*, (c) a double endopodite consisting of an inner *lacinia* and a softer outer *galea*. Behind the maxillæ lies a pair of appendages which correspond in position to the first maxillipeds of the crayfish, but are here known sometimes as the second maxillæ, though better as the *labium*. Their protopodites are fused so that they form a single lower lip. The first joint of their common protopodite is the *submentum*, the second the *mentum*. This bears on each side an exopodite or *labial palp* of three joints, set upon a projection of the mentum known as the *palpiger*. At the end of the mentum stand the two endopodites. Their basal parts are fused, like the protopodites, forming a structure, known as the *ligula*, which is deeply notched at its free end. On each side of the notch it bears an inner lacinia and an outer *paraglossa*. It will be seen that the head of the cockroach contains one segment more than that of the crayfish.

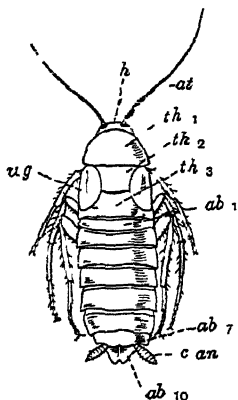


FIG 147 — A female of the common cockroach (*P. orientalis*). The body is somewhat compressed so as to show the membranes between the abdominal terga. The legs are not in the attitude characteristic of the living animal.

ab 1-ab 10, Abdominal terga
at antenna can anal
cerci h, head th 1 pro
thoracic tergum th 2
mesothoracic tergum th 3,
metathoracic tergum wg,
vestige of fore wing

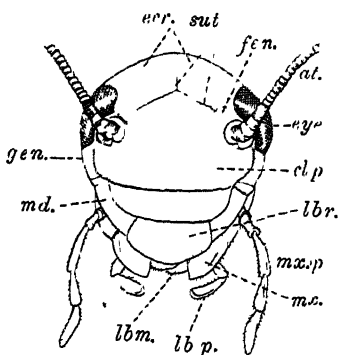


FIG. 148.—The head of a cockroach, seen from in front.

at, Antenna; *clp.*, clypeus; *ecr.*, epicranium; *eye*; *fen.*, tenestra; *gen.*, gena; *lbm.*, part of the labium; *lb.p.*, labial palp; *lbr.*, labrum; *md.*, mandible; *mx.*, part of the maxilla; *mx.p.*, maxillary palp; *sut.*, sutures.

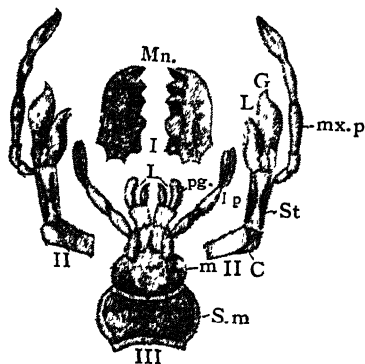


FIG. 149.—The mouth appendages of a cockroach.—After Dufour.

I. *Mn.*, mandibles; II maxillæ, *C.*, cardo; *St.*, stipes; *L.*, lacinia; *G.*, galea; *mx.p.*, maxillary palp; III. labium, *S.m.*, submentum; *m.*, mentum; *L.*, lacinia; *pg.*, paraglossa; *l.p.*, labial palp.

The head is joined by a soft neck to the thorax.

Thorax. This consists of three segments — the prothorax, mesothorax, and metathorax. Each has a tergum or *notum* above and a sternum below. The pronotum is the largest and projects in front so as to hide the neck. Each segment bears a pair of legs. The shape of these legs and the names of their joints are shown in Fig. 151. The third and fourth joints bear bristles which are used in cleaning the body, and the last joint bears two hooked claws used in climbing and between the claws a pad or *pulvillus* which prevents slipping. The mesothorax and metathorax bear each a pair of wings jointed to the anterior corners of the notum. The wings are membranous folds of the cuticle strengthened by ridges known as *nerve*ures. The first pair are dark coloured and horny and form a cover for the second, which, when they are at rest, are folded lengthwise and

laid along the back. In the female of *P. orientalis* the wings are very small. Wings are not appendages of the same kind as the limbs, but movable expansions of the terga.

The abdomen consists of ten segments, each with a tergum and a sternum, joined at the sides by soft cuticle. The hinder segments are telescoped, so that the eighth and ninth are hidden.¹ The first

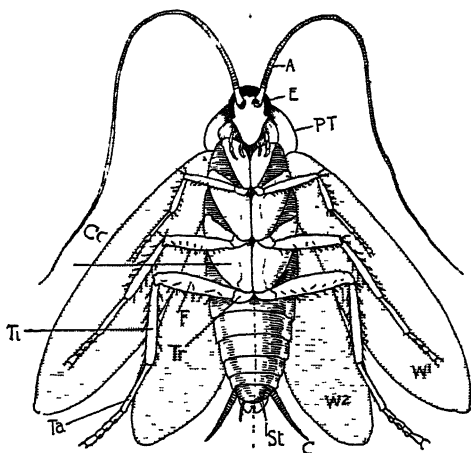


FIG. 150.—The ventral aspect of a male cockroach with the wings extended. An imaginary median line has been inserted.—From Thomson.

A., antennæ; C., cercus; Co., coxa; E., eye; F., femur; P.T., prothorax; St., style; Ta., tarsus; Ti., tibia; Tr., trochanter; W¹, first pair of wings; W², second pair of wings.

sternum is rudimentary, and the tenth tergum projects backwards as a plate with a deep notch in its hinder edge. A pair of many-jointed, spindle-shaped *cerci anales*, which may represent limbs, are attached under this plate, and below it is the anus, between two *podical plates*, which may represent the tergum of an eleventh segment. In the female the seventh sternum is produced backwards into a large boat-

¹ In the male *P. orientalis* portions of the eighth and ninth terga remain uncovered.

shaped process, which forms the floor of a *genital pouch*, and in the male the ninth sternum bears a pair of slender, unjointed *styles*. The genital opening is placed below the anus and is surrounded by a complicated set of processes known as *gonapophyses*.

The alimentary canal has long, ectodermal fore- and hind-guts, lined with cuticle as in the crayfish. The fore-gut comprises (i) the mouth, with a tongue-like ridge and the opening of the duct of the salivary glands, (ii) the narrow gullet, lying in the neck, (iii) the swollen crop, (iv) the proventriculus or gizzard, which has muscular walls and contains six hard, cuticular teeth

Alimentary System.

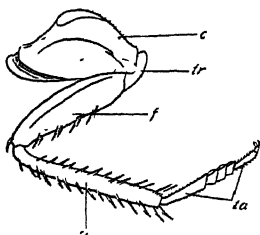


FIG. 151.—The leg of a cockroach.—From Thomson.

, Broad expanded coxa; *f.*, femur; *ta*, six-jointed tarsus with terminal claws and adhesive cushions; *tt*, tibia; *tr.*, trochanter.

and some pads covered with bristles which form a strainer. The mid-gut or mesenteron, lined by soft endoderm, is short and narrow and bears at its beginning seven or eight club-shaped *hepatic caeca*, which secrete a digestive fluid. The gizzard projects funnel-wise into the mid-gut. The hind-gut is coiled and divided into a narrow ileum, a wider colon, and a still wider rectum, which has six internal ridges. A pair of diffuse salivary glands lie on

each side of the gut, and between each pair lies a salivary bladder or receptacle. The ducts of the two glands of each side join; the ducts of the two sides then unite to form a median duct, and this is joined by another median duct formed by the union of the ducts of the receptacles. The common duct opens into the floor of the mouth between the tongue and the lower lip. At the beginning of the hind-gut a number of long, fine *Malpighian tubules* are attached. They have an excretory function, and their lumina often contain uric acid which has been shed out by the glandular epithelium which lines them.

The respiratory system consists of branching tubes or *tracheæ*, with a spirally thickened chitinous lining, which

cavity. The perivisceral and pericardial spaces contain a white tissue known as the *fatty body*, which appears, among other functions, to play some part in the formation of uric acid.

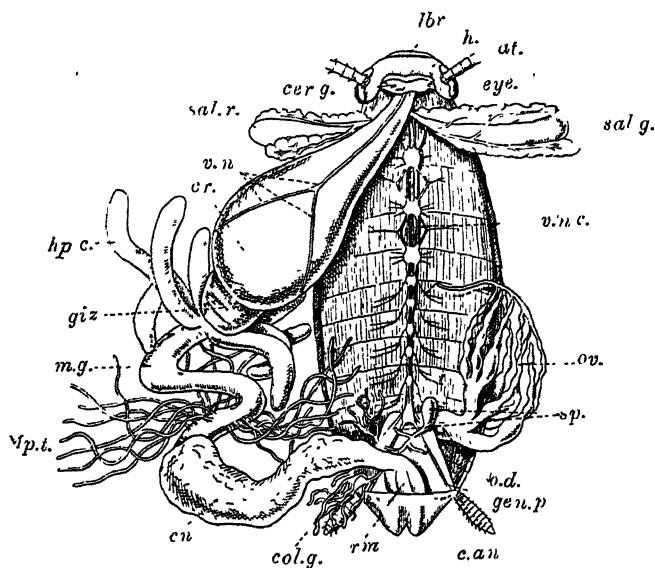


FIG. 153.—A female cockroach, dissected from above.—From Shipley and MacBride.

at., Antenna; *c.an.*, anal cerci; *cer.g.*, cerebral ganglia; *cn*, colon; *col.g.*, colateral gland; *cr.*, crop; *eye*, eye; *gen.p.*, genital pouch; *giz.*, gizzard; *h.*, head; *hp.c.*, hepatic cocca; *lbr.*, labrum; *m.g.*, mesenteron; *Malp.t.*, Malpighian tubes; *o.d.*, oviduct; *ov.*, ovary; *rm.*, rectum; *sal.g.*, salivary glands; *sal.r.*, salivary receptacle; *sp.*, spermathecae; *v.n.*, visceral nerves; *v.n.c.*, ventral nerve cord.

The nervous system is on the same general plan as that of the crayfish. It comprises a pair of supra-oesophageal ganglia, which receive optic and antennary nerves, a pair of short, wide circum-oesophageal commissures, a suboesophageal ganglion, and a double ventral cord with a ganglion in

**Nervous
System and
Sense Organs.**

each of the first nine segments behind the head. The alimentary canal is supplied by a visceral nervous system which receives nerves from the circumœsophageal commissures and the brain. Its principal ganglion lies on the upper side of the crop. The sense organs include the large compound eyes, which resemble those of the crayfish in structure, the antennæ, which are tactile and olfactory, the maxillæ, which are said to possess the sense of taste, the tactile anal cerci, various sensory bristles, and possibly a pair of oval, white patches on the head, above the bases of the antennæ, known as the *fenestræ*.

The sexes are separate. The testes are small, paired

organs, embedded in the fatty body below the fifth and sixth abdominal terga. In the adult they are no longer functional. Two vasa deferentia lead backwards and downwards from them to the seminal vesicles, which are beset with short finger-like processes and lie side by side to form the so-called *mushroom-shaped gland*.

The seminal vesicles join behind to form a muscular tube, the *ductus ejaculatorius*, which opens by a median pore between the ninth and tenth abdominal sterna. A gland of doubtful function, known as the *conglobate gland*, lies below the ductus ejaculatorius and opens with it. The ovaries are paired organs in the hinder part of the abdomen, each consisting of eight tubes, which show swellings corresponding to a row of ova. There is a single, short, wide oviduct which opens on the eighth abdominal sternum. On the ninth sternum a pair of branched *colleterial glands* pour out by two openings a secretion which forms the egg-cases. There is an unequal pair of sperma-

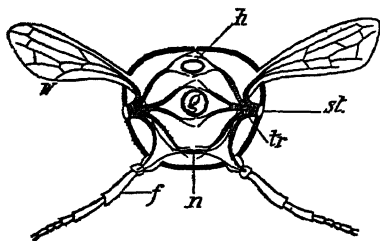


FIG. 154.—A diagram of a transverse section of an insect.—After Packard.

f., Femur of leg; g., gut; h., heart; n., nerve-cord; st., stigma; tr., trachea; w., wing.

thecæ which open between the eighth and ninth abdominal sterna. The eggs are laid in cases containing sixteen ova and some spermatozoa from the spermathecæ. The young are like the adults, save for the absence of the wings, which appear at the last of a series of moults. Thus the

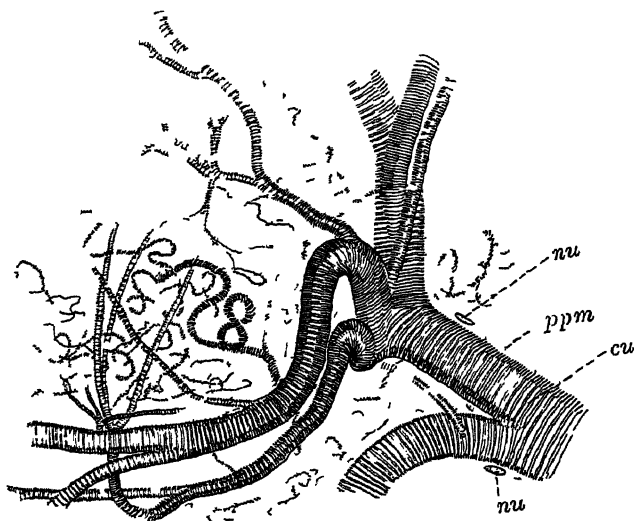


FIG 155 —A portion of the tracheal tissue of a cockroach, highly magnified. Only parts of the tubes are in focus.

cu, Cuticular lining with spiral thickening. *nu*, nuclei of the protoplasmic layer, *ppm*, protoplasmic layer continuous with the epidermis ("hypodermis") of the surface of the body.

metamorphosis found in so many insects is practically absent.

The number of different kinds of insects is enormous. Probably it is not less than 500,000 and equals that of all other animals together. All insects resemble the cockroach in the main features of their anatomy, but many of them depart widely from it in detail, the differences affecting

principally the mouth parts, the wings, and the life-history. The mouth-parts vary in structure with the way in which they are used. In some cases, as in Beetles, they are not very unlike those of the cockroach, and are used for biting the food. In others, as in Bugs and Flies, they are adapted for piercing the bodies of other organisms, animals or plants, and sucking their juices, the labium forming a tube in which lie the other parts in the form of slender knives or needles. In Butterflies the

maxillæ are long and grooved, and placed against one another so as to form a tube or proboscis through which nectar can be sucked from flowers, the other mouth parts being vestigial with the exception of the labial palps. In Bees the mouth parts are adapted for biting and sucking, the mandibles being not unlike those of a cockroach, the

lacinix of the maxillæ blade-like, and those of the labium forming a grooved structure, along which liquids can be drawn up. Wings are occasionally absent. They may both be gauzy and used in flight, or, as in beetles, the first pair may be hard and horny and form a case for the second, or, as in flies, the first pair alone may be used in flight and the second pair represented by two minute balancers or halteres. In butterflies both pairs are covered, like the rest of the body, with little scales, which can be brushed off as a powder.

The life histories of insects are of three types (1) In

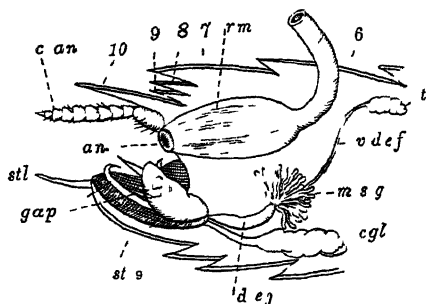


FIG 156 — A semi diagrammatic view of the hinder part of the body of a male *P. americana* dissected from the right side to show the generative organs

an, Anus can, anal cerci cgl, conglobate gland, dej, ductus ejaculatorius gap, gonapophyses, ms g, mushroom shaped gland rm, rectum st 9, ninth sternum stl, style, t, testis, v def, vas deferens 6 to, terga

laciniæ of the maxillæ blade-like, and those of the labium forming a grooved structure, along which liquids can be drawn up. Wings are occasionally absent. They may both be gauzy and used in flight, or, as in beetles, the first pair may be hard and horny and form a case for the second, or, as in flies, the first pair alone may be used in flight and the second pair represented by two minute balancers or halteres. In butterflies both pairs are covered, like the rest of the body, with little scales, which can be brushed off as a powder.

The life histories of insects are of three types (1) In

certain cases, known as *Epimorpha*, the young differ only slightly from the adults, into which they change gradually

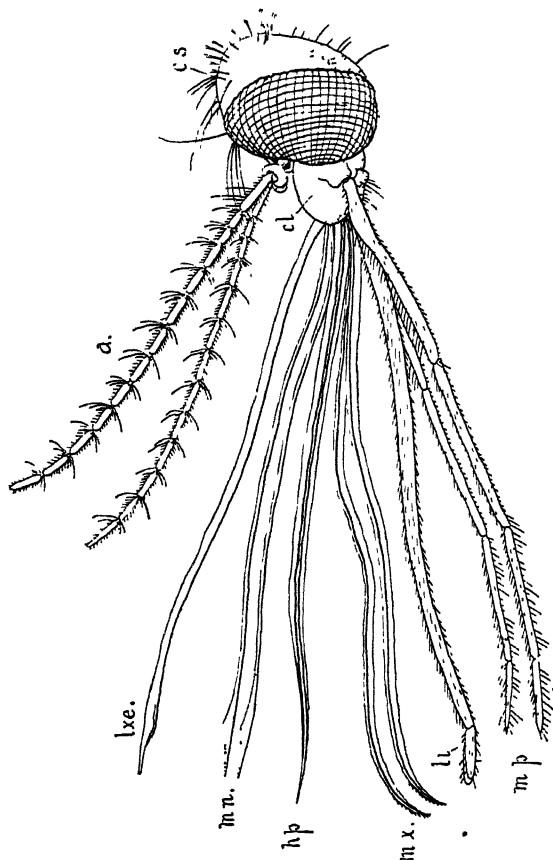


FIG. 157.—The mouth-pairs of a mosquito.—After Nuttall and Shipley.

a., Antennae; *lxe.*, labrum and epipharynx; *mn.*, mandibles; *lp.*, hypopharynx; *mt.*, first maxillae, *li.*, labium; *mp.*, maxillary palps; *cl.*, clypeus; *cs.*, head scales.

by a series of moults, acquiring at each certain of the adult organs. This occurs in the cockroach
Life Histories. and insects related to it, in bugs, etc. In other cases the young differ considerably from the adult,

and the change from one to the other takes place at a definite stage in the life-history. A young animal which

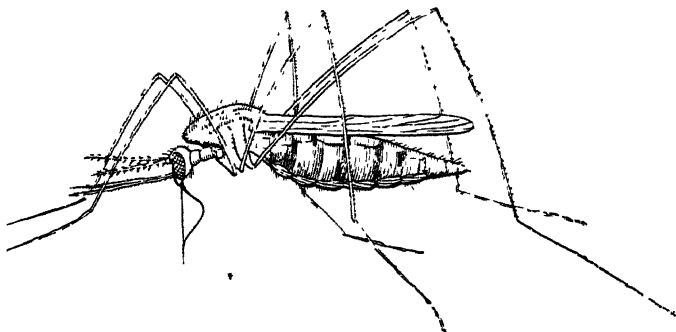


FIG. 158.—A mosquito, sucking blood.—After Nuttall and Shipley.
The curved line under the head is the labium.

differs markedly from the adults of its species and lives an independent life is known as a *larva*. We have already seen an instance of a larva in the tadpole. The term *embryo* is applied to a young organism while it is developing within the body of its parent or under shelter of an egg shell, like the young of man or birds or the early stages of insects. The change by which a larva becomes an adult is known as its *metamorphosis*. The adult form of an insect is known as its *imago*, and the epimorpha are said to have an *incomplete metamorphosis*. Other insects have a larval stage and a more or less *complete metamorphosis*. (2) In dragonflies and certain other insects, at the stage in which the metamorphosis takes place the animal is free and active and is known as a *nymph*. *Hemimetabola*. (3) In the rest of the insects, including

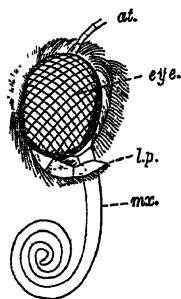


FIG. 159.—A side view of the head of a butterfly.

at., Antenna; eye; l.p., labial palp; mx., maxilla.

Such insects are

beetles, ants, bees and wasps, flies and butterflies, the insect passes through an almost motionless stage known as the *pupa*. These insects are called *Holometabola*, and in them the metamorphosis is very complete. The body of the pupa undergoes a profound reorganisation. A few of the most important systems of organs, such as the reproductive, nervous, and circulatory, last on, but the others are devoured by a phagocytic action (p. 98) of the blood corpuscles and re-formed by the growth of certain clumps of cells, known as *imaginal discs*, which have retained the

embryonic power of growing into new organs. The larvæ of insects differ greatly. They may resemble the imago in the general shape of the body, as in dragonflies and some beetles (Fig. 163, L), or they may be caterpillar-like and have the thorax ill-marked, as in butterflies, sawflies, etc. (Fig. 163, A), or they may be mere grubs, as in many flies, bees, etc. (Fig. 163, J).

According to these and other characters the principal kinds of

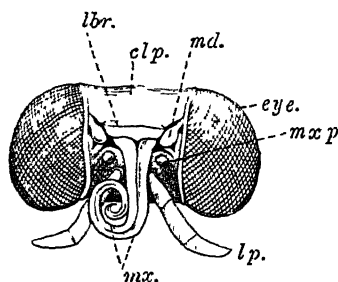


FIG. 160.—The head of a tiger moth (*Arctia caja*), seen from in front and partly from below, after the removal of the scales.

clp., Clypeus; *eye.*, eye; *lp.*, labial palp; *lbr.*, labrum, *md.*, structure supposed to represent a mandible; *mx.* maxillæ; *mx p.*, maxillary palp.

insects may be classified as follows:—

1. *Orthoptera*.—Jaws adapted for biting, wings usually unlike. Metamorphosis incomplete. Cockroaches, Grasshoppers, etc.

2. *Neuroptera*.—Jaws either for biting or for sucking. Wings alike, membranous. Metamorphosis various. Dragonflies, Mayflies, etc.

3. *Coleoptera*.—Jaws for biting. First pair of wings form a hard cover for the membranous second pair. Metamorphosis complete. Beetles.

4. *Hymenoptera*.—Jaws for biting and sucking. Four membranous wings. Metamorphosis complete. Many live

in communities, the majority of the members of which are sterile females or "workers." Bees, Wasps, Ants, Sawflies.

5. *Hemiptera*.—Jaws for piercing and sucking. Wings alike or different. Metamorphosis incomplete. Bugs, Plantlice, etc.

6. *Diptera*.—Jaws for piercing and sucking. Hind wings represented by minute balancers, fore wings membranous. Metamorphosis complete. Flies, Gnats, Mosquitoes, Crane-flies, etc.

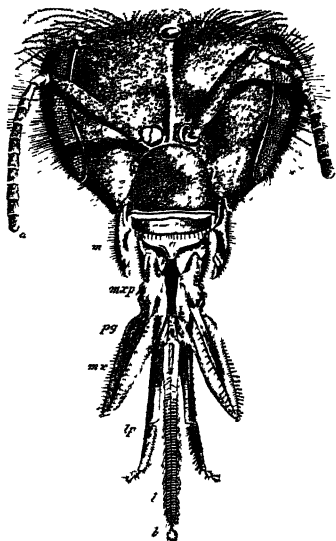


FIG. 161.—The head and mouth-parts of a bee. — After Cheshire.

a., Antenna; *m.*, mandible; *g.*, labrum or epipharynx; *mxp.*, rudiment of maxillary palp; *mx.*, lamina of maxilla; *lp.*, labial palp; *l.*, ligula; *b.*, bouton at end. The paraglossæ lie concealed between the basal portions of the labial palps and the ligula.

7. *Lepidoptera*.—Jaws for sucking, formed by the maxillæ only. Four wings alike and covered with scales, as is also

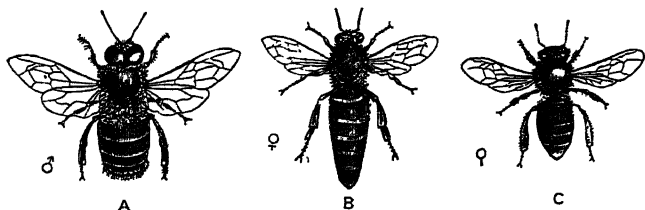


FIG. 162.—The honey bee.—From Shipley and MacBride.

A, Male or drone; *B*, female or queen; *C*, sterile female or worker.

the body. Metamorphosis complete. Butterflies and Moths.

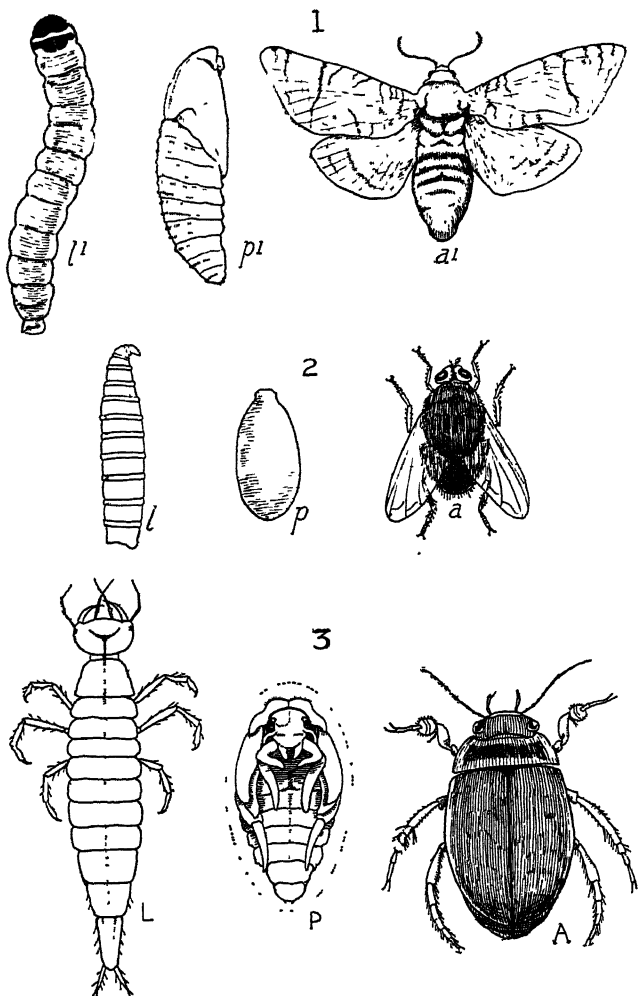


FIG. 163.—Life-histories of Insects.—From Thomson.

L., *P.*, and *A*, larva, pupa, and adult respectively of the great water-beetle (*Dytiscus marginalis*); *l.*, *p.*, *a*, larva, pupa, and adult of the blue-bottle fly (*Musca vomitoria*); *l.*, *p.*, *a*, larva, pupa, and adult of the goat moth (*Cossus ligniperda*)

CHAPTER XVI

THE SWAN MUSSEL

FRESHWATER mussels may be found in most streams, canals, and large ponds in Britain, though they are often overlooked on account of their habit of burying themselves in the mud with at most a small part of the body projecting. The commonest of them is the Swan Mussel, *Anodonta cygnea*. When it is removed from the mud it is seen to be enclosed in a flat, dark green shell, four to six inches long and roughly oval in outline, with one end (the front) rounded and the other more pointed. The shell consists of two similar pieces, known as *valves*, which lie one on each side of the animal joined by a hinge above the back, where their edges are almost straight. On being disturbed the mussel holds the valves tightly together, but when it is at rest in the water they gape somewhat, and at the hind end, which projects slightly from the mud, there may be seen between them two fleshy lobes enclosing an opening shaped like a figure of 8, through one of whose limbs a current sets into the shell, while through the other, the upper of the two, the water is driven out. At times the animal moves about, thrusting out a yellowish, ploughshare-shaped organ known as the *foot*, with which it ploughs its way through the mud at the rate of about a mile a year. Freshwater mussels are not unfit for food and are sometimes eaten. They are preyed upon by water-fowl and other animals, and in places are fished for on account of the pearls which they contain, which may be of considerable value. They are not killed by the freezing of the water even if they themselves be frozen solid, but can only survive a few hours of drought.

The shell consists of an outer horny layer, the *periostracum*,

a thick middle *prismatic layer* impregnated with salts of lime, and an inner *nacreous* layer of mother-of-pearl, which consists of thin calcareous laminae. *Lines of growth* parallel with its edge mark the outside of the shell, centering upon a point about a quarter of its length from the front end. This point is known as the *umbo* and shows the position of the first shell

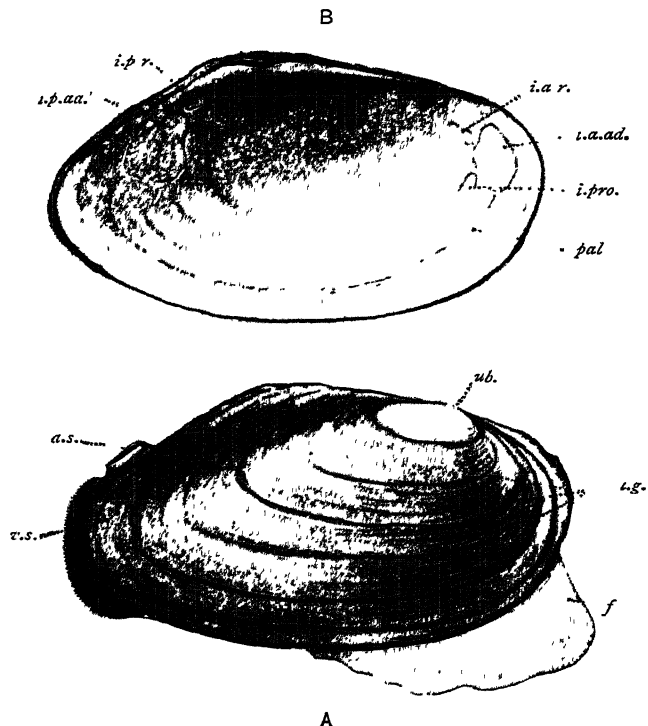


FIG. 164.—The Swan Mussel.

A, The shell with the animal, from the right side; *B*, the left valve of the shell, from within

d.s., Dorsal siphon; *f.*, foot; *i.*, impressions of muscles; *i.a.ad.*, of anterior adductor; *i.a.r.*, of anterior retractor; *i.p.ad.*, of posterior adductor; *i.p.r.*, of posterior retractor; *i.pro.*, of protractor; *l.g.*, lines of growth; *pal.*, pallial line; *ub.*, umbo; *v.s.*, ventral siphon.

of the young mussel. On the inside of the shell may be seen the *marks of attachment* of the adductor, retractor, and protractor muscles presently to be mentioned, and parallel with its edge is a mark known as the *pallial line*, where the fold of the body-wall known as the mantle is attached. Above the hinge the two valves are joined by an elastic ligament, which pulls them together above and thus opens them below when the adductor muscles are relaxed. To open the shell of a living mussel the blade of a knife is passed between the valves and they are prised apart till the muscles can be cut close to the shell on one side.

The body of the animal is then found to be soft, without a cuticle, and provided with a flap of tissue which hangs down on each side and covers the other organs. This is the *mantle*. It has a thick edge which secretes the two outer layers of the shell, while the pearly layer is laid down by the whole surface of the mantle and skin of the back. Its origin from the side of the body is not straight but higher in the middle than near the two ends, though at

the extreme ends it turns upwards to the hinge line. At the hind end each mantle edge is fused for some distance with its fellow; it then separates widely from it twice, so as to form the figure of 8 already mentioned, and lies against its fellow for the rest of its length. The upper opening is known as the *dorsal siphon*, the lower as the *ventral siphon*. The lips of the latter bear a fringe of small tentacles. The space enclosed by the two *mantle lobes* is known as the *mantle cavity*.

It will have been noticed that the shell and mantle of the mussel are bilaterally symmetrical. The same symmetry is found in all the other organs of the body,

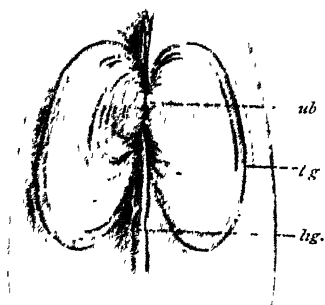


FIG. 165.—Part of the shell of a swan mussel, seen from above.

lg., Lines of growth; *hg.*, ligament;
ub., umbo.

both internal and external. Above the attachment of the mantle, at its lowest point near each end, may be seen on each side the cut surface of the great *adductor muscles*, anterior and posterior, which pass through the body from side to side and draw together the valves of the shell. To the upper and inner sides of these lie the anterior and posterior

**External Features:
Locomotion
and Feeding.**

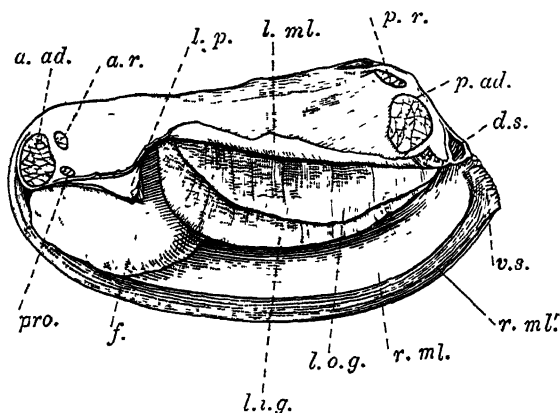


FIG. 166.—A swan mussel removed from its shell and lying on its right side with the greater part of the left lobe of the mantle cut away.

a. ad., Anterior adductor muscle; *a. r.*, anterior retractor; *d. s.*, dorsal siphon; *f.*, foot; *l. i. g.*, left inner gill; *l. ml.*, remains of left mantle lobe turned back; *l. o. g.*, left outer gill; *l. p.*, labial palps; *p. ad.*, posterior adductor muscle; *p. r.*, posterior retractor; *pro.*, protractor; *r. ml.*, right mantle lobe; *r. ml.*, thickened edge of the same; *v. s.*, ventral siphon with papillae

retractor muscles, which draw the body forwards upon the foot when the latter has been thrust out. Behind the lower end of each anterior adductor is a *protractor muscle*, which draws the body backward upon the foot. On turning back the mantle the rest of the external organs are laid bare. The most conspicuous of these are the foot and two pairs of flaps which hang down on each side of the body. One pair is large, extends from the hind end along the greater part of the length of the animal, and consists of

the gills. The other is smaller, lies in front of the gills, and is known as the labial palps. The foot is a compressed structure, with a point directed forwards, lying under the front half of the body. Its lower part is muscular, its upper part soft, containing the genital organs and intestine. It is thrust out between the valves by the forcing of blood into the sinuses which it contains, and withdrawn by the

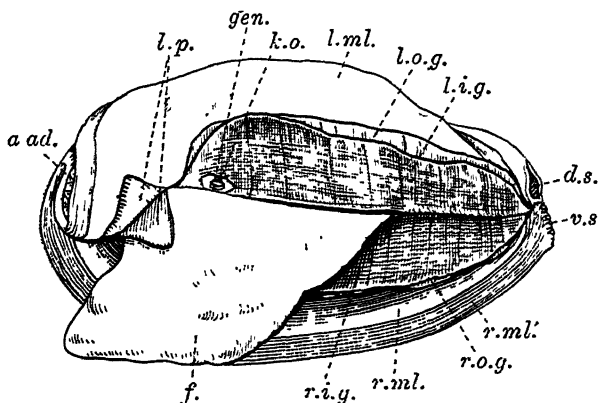


FIG. 167.—A swan mussel removed from its shell and lying on its right side with the left mantle lobe and left gills turned back. A portion of the inner lamella of the left inner gill has been cut away to show the openings of the kidney and gonad.

a.ad., Anterior adductor muscle; *d.s.*, dorsal siphon; *f.*, foot; *gen.*, opening of the duct of the gonad; *k.o.*, opening of the kidney; *l.i.g.*, left inner gill; *l.ml.*, left mantle lobe; *l.o.g.*, left outer gill; *l.p.*, labial palps; *r.i.g.*, right inner gill; *r.ml.*, right mantle lobe; *r.ml.*, thickened edge of the same; *r.o.g.*, right outer gill; *v.s.*, ventral siphon.

removal of the blood by the action of its muscles. In locomotion it is wedged into the mud or between stones, and the body is then drawn forwards upon it by the retractor muscles. Above the foot, between it and the anterior adductor muscle, lies the mouth, bordered by upper and lower lips. At the sides of the mouth these lips are continuous with the *labial palps*, which are a pair of triangular flaps, one outside the other, on each side of the body, the outer palps being joined in front of the mouth

by the upper lip and the inner behind the mouth by the lower lip. The palps are ciliated, and their surfaces which are towards one another are crossed by fine furrows, which lead upwards towards the groove between them. This is continuous with the corners of the mouth, and the whole forms an apparatus by which small organisms and other fine organic particles are gathered from the water in the mantle cavity and swallowed. Each of the *gills* consists of two *lamellæ* continuous along their ventral edges. As there are two gills on each side of the body,

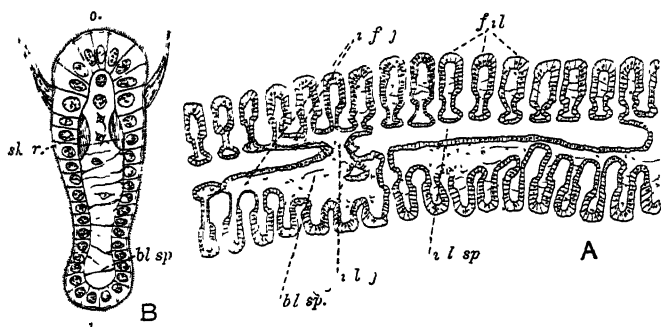


FIG. 168.—*A*, A horizontal section through a gill of the swan mussel, under low magnification; *B*, a single filament of the same, more highly magnified.

bl.sp., Blood spaces; *fil.*, filaments; *ifj.*, interfilamentar junction, *ilj.*, interlamellar junction; *i.l.sp.*, interlamellar space; *o.*, outer side of filament; *sk.r.*, sections of the chitinous skeletal rods which support each filament.

there are on each side four lamellæ. Each lamella is composed of very numerous vertical *filaments* whose inner sides (that is, the side of each towards the other lamella) are fused together at irregular intervals, so as to form a ribbed plate pierced by numerous openings between the ribs leading into the *interlamellar space* of the gill. The filaments of the two lamellæ of a gill are continuous, each filament passing down one lamella and up the other, so that the whole gill may be said to be composed of a number of bent filaments fused side by side so as to form two lamellæ. The two lamellæ of each gill are connected

at intervals by thick vertical ridges parallel to the filaments. The lamellæ diverge upwards, so that in transverse section the two gills of each side have the form of a W. The space into which each interlamellar space widens at the top is known as an *epibranchial space*. The outer lamella of the outer gill of each side is attached along the whole length of its upper border to the inner surface of the mantle, close to the origin of the latter from the body-wall. The inner lamella of the outer gill is attached along the whole length of its upper edge to the outer lamella of the inner gill.

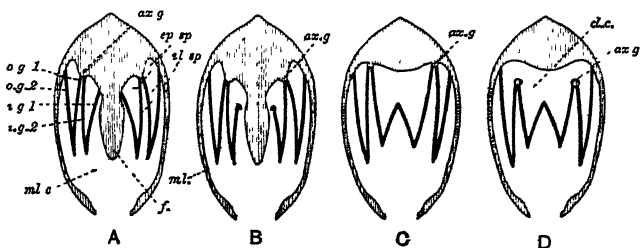


FIG. 169.—Diagrams of transverse sections through the swan mussel.

A passes through the middle of the foot and shows the inner lamella of the inner gill attached to the side of the foot; *B* passes through the hinder part of the foot and shows the inner lamella of the inner gill free; *C* is taken behind the foot and shows the inner lamellæ of the inner gills joining in the middle line; *D* is further back and shows the axes of the gills free.

ax.g., Axes of the gills; *cl.c.*, cloacal chamber; *ep.sp.*, epibranchial space; *f.*, foot; *i.g.1*, inner lamella of inner gill; *i.g.2*, outer lamella of inner gill; *il.sp.*, interlamellar space; *o.g.1*, inner lamellæ of outer gill; *o.g.2*, outer lamella of outer gill; *ml.*, mantle lobe; *ml.c.*, mantle cavity.

The line of their junction is thickened and may be called the *axis* of the gills. The axis is attached for most of its length to the ventral side of the body, but behind becomes free. The inner lamella of the inner gill is attached in front to the top of the foot, its middle portion has a free edge, and behind the foot it is attached to its fellow of the opposite side. The result of this arrangement of the attachments of the gills is that the epibranchial spaces, which are separate in front, join behind to form a *cloacal space* which communicates with the outside by the dorsal siphon. Into this space opens the anus, which is placed above the posterior adductor muscle. The surface of the gills is covered with

strong cilia, which set up a current of water through the perforations of the lamellæ into the interlamellar spaces and so by way of the epibranchial and cloacal spaces to the exterior at the dorsal siphon. The current is maintained by the entry of water at the ventral siphon, where it passes over the tentacles, which test its purity, causing if necessary a sudden closure of the valves which drives water out at both siphons and washes any obnoxious substance away. The continual renewal of the water brings fresh supplies of oxygen to the gills and food to the labial palps, and the outgoing current bears away carbon dioxide from the gills and mantle surface, fæces from the anus, and excreta from the kidneys, which, as we shall see, open into the inner epibranchial chambers at their front ends.

The swan mussel is a coelomate animal, intermediate between the earthworm and the crayfish in respect to its coelom and hæmocœle. It has a perivisceral coelom, situated in the back, enclosing the heart and rectum and communicating with the exterior by an excretory tube on each side. This space is known as the pericardium. In the rest of the body the organs are separated by blood sinuses, the circulation being an open one. The gonads represent a part of the coelom. Most of the viscera lie in the upper part of the body, known as the *visceral hump*, but the gonads and intestine lie in the soft region of the foot. The mouth leads into a gullet, which passes upwards into a moderate-sized stomach behind the anterior adductor muscle. Into the stomach is poured by several ducts the secretion of a large digestive gland which surrounds it. An intestine starts from the lower side of the stomach, takes several coils in the soft upper part of the foot, turns upwards, and runs straight backwards in the middle line of the upper part of the body to the anus. The straight part of the intestine is known as the rectum. It lies in the pericardium surrounded by the ventricle of the heart. The ventral wall of the rectum is folded to form a longitudinal ridge or typhlosole.

The kidneys or *organs of Bojanus* are two in number and lie side by side below the pericardium. Each is a wide tube, doubled on itself, with one limb above the

other, and the two ends together in front. The lower limb has spongy walls lined with a dark, glandular epithelium. It opens into the front end of the pericardium by a crescentic *renopericardial opening* in the floor of the latter. The upper limb has thin walls. It opens on the side of the body

**Excretory
Organs and
Gonads.**

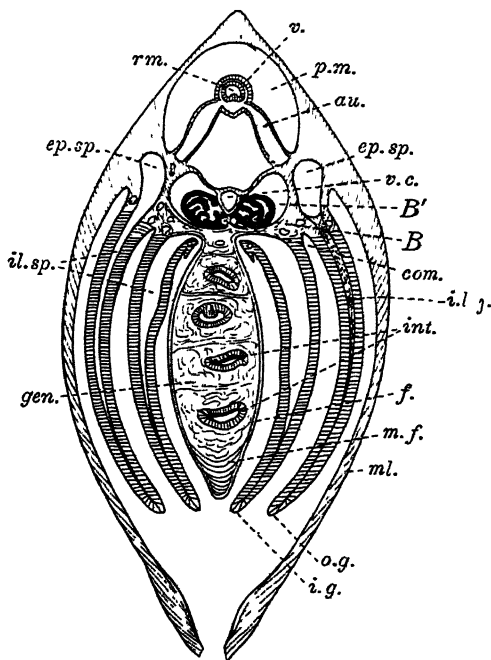


FIG. 170.—A semi-diagrammatic drawing of a transverse section of the swan mussel in the region of the hinder part of the foot.

au., auricle; *B*, glandular limb of kidney; *B'*, non-glandular limb of the same; *com.*, commissures between cerebral and parietosplanchnic ganglia; *ep.sp.*, epibranchial spaces; *f.*, foot; *gen.*, gonad; *i.g.*, inner gill; *i.l.j.*, interlamellar junction; *il.sp.*, interlamellar spaces; *int.*, intestine; *m.f.*, muscular part of the foot; *ml.*, mantle lobe; *o.g.*, outer gill; *p.m.*, pericardium; *rm.*, rectum; *v.*, ventricle; *v.c.*, vena cava.

into the adjoining inner epibranchial chamber, shortly before the point at which the inner lamella of the inner gill becomes free. Thus the two ends of the kidney tube cross, the lower opening upwards and the upper downwards. It should be noted that the swan mussel, like the earthworm,

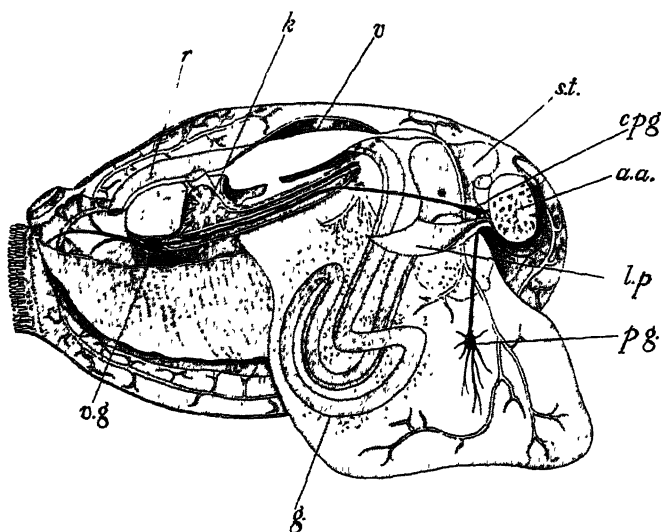


FIG. 171.—The structure of *Anodonta*.—After Rankin.

a a., Anterior adductor; *cp.g.*, cerebral or cerebropleural ganglia; *st.*, stomach; *v.*, ventricle, with an auricle opening into it; *k.*, kidney, above which is the posterior retractor of the foot; *r.*, rectum ending above posterior adductor; *v.g.*, visceral ganglia with connectives (in black) from cerebropleurals; *g.*, gut coiling in foot; *p.g.*, pedal ganglia in foot, where also are seen branches of the anterior aorta and the reproductive organs; *l.p.*, labial palps behind mouth. At the posterior end the exhalant (upper) and inhalant (lower) siphons are seen.

the tadpole, and probably the crayfish, possesses excretory organs in the form of coiled tubes which open at one end into the coelom and at the other communicate with the exterior. A pair of glandular bodies known as *Keber's organs* lie one on each side in front of the pericardium and pass into it waste products which they excrete. They are derived from the coelomic wall and, like the yellow cells of the earthworm,

represent a portion of its epithelium specialised for excretion. The opening of the kidney has thick, yellowish lips. Immediately below it is a somewhat larger opening with thin lips. This belongs to the gonad, which is a branched structure lying in the upper part of the foot and alike in its general structure in both sexes.

The blood is colourless and contains white corpuscles.

Vascular System.

The heart consists of a ventricle, which forms a jacket around the rectum, and two auricles, which are triangular, thin-walled structures, one on each side of the ventricle. From the front end of the

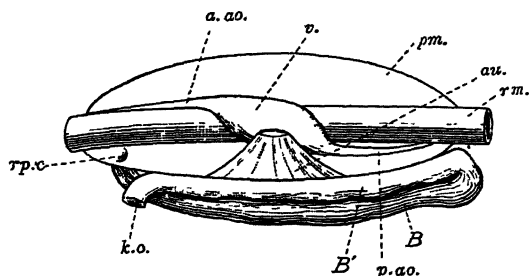


FIG. 172.—A diagram of the pericardium and kidney of the swan mussel, from the left side.

a.ao., Anterior aorta; *au.*, auricle; *B*, glandular limb of kidney; *B'*, non-glandular limb of the same; *k.o.*, opening of the same; *p.ao.*, posterior aorta; *pm.*, pericardium; *rp.o.*, renopericardial opening; *rm.*, rectum; *v.*, ventricle.

ventricle an *anterior aorta* passes forwards above the rectum, and from the hind end a *posterior aorta* passes backward below it. From branches of these the blood passes into spaces between the organs. From the foot and viscera it is gathered into a *vena cava* which lies below the pericardium between the kidneys. Thence it passes outwards through the kidneys to the gills, where it circulates in irregular spaces in the inner parts of the filaments. From these it is returned to the auricles. The blood from the mantle returns direct to the auricles.

The nervous system consists of three pairs of ganglia with commissures uniting them. The *cerebral ganglia* are two small, orange-coloured bodies, placed one on each

side behind the mouth, above which they are connected by a *cerebral commissure*. They supply the fore part of the body, and each gives off a *cerebro-pedal commissure* to one of the two *pedal ganglia* which lie side by side in the foot, just above the muscular region, about one third of the length of the organ from its front end. The pedal ganglia bear the same relation to the

**Nervous
System**

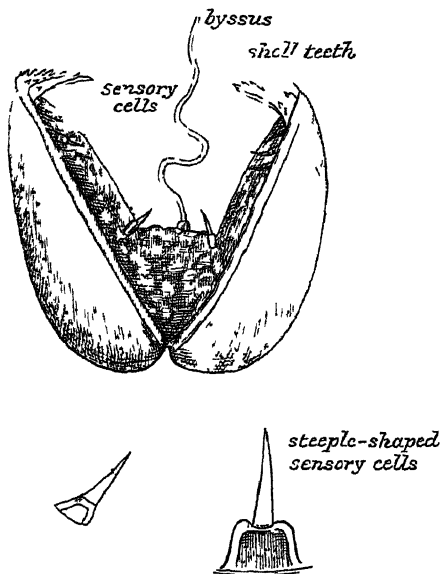


FIG 173 —A glochidium larva, as cast out from the parent, viewed from behind —From Latta

cerebral that the subpharyngeal do to the suprapharyngeal in the earthworm. The pedal ganglia give off several nerves to the foot, and each sends a nerve to a *statocyst* which lies shortly behind it. Each cerebral ganglion also gives off a *visceral commissure*, which runs backwards between the kidneys to join one of the *visceral or parietosplanchnic ganglia* which lie as a fused pair on the under side of the posterior adductor muscle, immediately

within the skin. The sense organs are inconspicuous. They include the statocysts, the tentacles of the ventral siphon, a sensory epithelium, believed to be olfactory, which covers the visceral ganglion and is known as the *osphradium*, and tactile nerve endings in various parts of the skin. There are no eyes.

The sexes of the swan mussel are separate. Sperm is passed out through the dorsal siphon and spermatozoa are drawn into the females with the inward stream. The eggs are fertilised in the cloacal

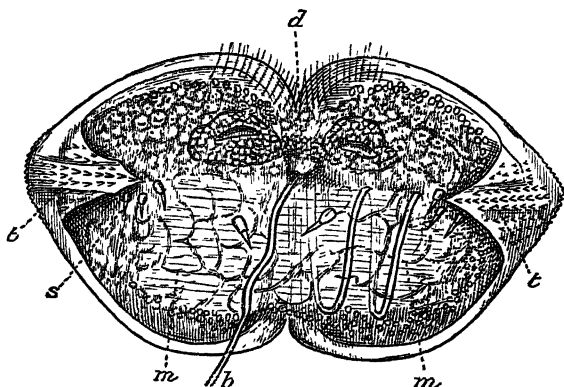


FIG. 174.—A glochidium larva in ventral view.—From Latter.

b., Byssus (cut short); d., future mouth; s., sensory cells; z., main teeth and denticles on ventral edge of each valve.

chamber and then passed into the space between the lamellæ of the outer gill, where they develop. This takes place in the summer. In the following spring the young are set free. They are larvæ, very unlike the parent, and are known as *glochidia*. Each has a shell composed of two triangular valves, hinged along the base and with the apex drawn out into a strong hook. There is no posterior adductor muscle, anus, or foot, but in the place of the latter is a gland which secretes a long sticky thread known as the *byssus*, comparable with the threads by which the adult sea mussel anchors itself. When some small fish, such as a stickleback, passes over the glochidium, it flaps its valves

so as to drive out the byssus, and if the latter touches the fish it sticks to it. The movements of the fish now bring the glochidium against its body, whereupon the hooks are used to hold on to its skin. The tissues of the fish become inflamed and swell up, enclosing the little parasite, which lives for some months by absorbing the juices of its host, during which time it undergoes a change into the adult form. Eventually the skin enclosing the young mussel withers and it drops off to lead an independent life. By means of this larva, the slow-moving mussel is dispersed into fresh feeding grounds by the fish, without the risk, which would be considerable if so small an organism were

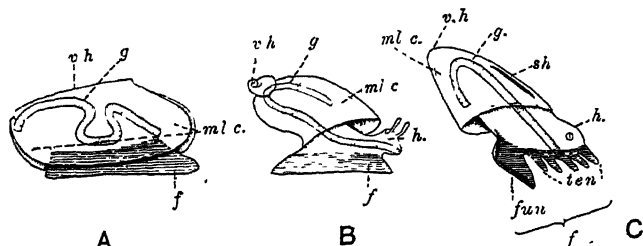


FIG. 175.—Diagrams of a mussel (A), a snail (B), and a cuttlefish (C).—Modified, after Lankester.

f., Foot; *fun.*, funnel through which water is squirted by the cuttlefish in swimming; *g.*, gut; *h.*, head; *ml.c.*, mantle cavity; *sh.*, internal shell found in some cuttlefish (the "cuttle bone"); *ten.*, tentacles of the cuttlefish; *v.h.*, apex of visceral hump.

free-swimming, of being carried downstream to the sea. We have seen that the young of the crayfish escape the same danger by holding on to the body of their mother. It is interesting to note that marine relations of both these animals have free-swimming larvæ.

Soft-bodied, shelled, unsegmented, cœlomate animals with a mantle, foot, and nervous system like those of the swan mussel are known as *Mollusca* or *true Shellfish*. Snails and Cuttlefish belong to this group. In a snail the body is flattened, not from side to side as in a mussel, but from above downwards, and the visceral hump is twisted. In a cuttlefish the body is flattened from before backwards. Snails and cuttlefish have heads, with eyes and a rough tongue or *radula*, which are wanting in mussels.

CHAPTER XVII

THE LANCELET

Habits and External Features. THE Common Lancelet, *Amphioxus lanceolatus*, is a little, fish-like creature found on most European coasts, including those of Britain, living in shallow water on a sandy bottom. It passes most of its time buried in the sand, with its length upright and the fore end projecting, gathering small organisms for food by a ciliated apparatus around the mouth. From time to time, usually at night, it leaves the sand, and then shows that it can swim swiftly by movements of its muscular body. It is about an inch and a half long, lustrous but translucent, slender, pointed at each end, and flattened from side to side. The head is in no way marked off from the rest of the body, and there are no ears, nostrils, or limbs. A low *dorsal fin* runs along the middle of the back from end to end, becoming deeper at the hinder end as the upper lobe of a *caudal fin*, which passes round the end of the tail. The under lobe of this is continuous with a low, median *ventral fin* which extends along the hinder third of the body. In front of the ventral fin the belly is flattened and bears at each side a continuous *lateral fin or metapleural fold*. The sides of the body are marked by a series of about sixty v-shaped lines, with their apices forwards, due to septa of connective tissue known as *myocommata*, which divide the muscles of the body-wall into segments called *myomeres*. Certain of the internal organs are repeated in correspondence with these, so that the body is segmented, though not so completely as that of the earthworm. The segmentation is peculiar in that the myotomes of opposite sides alternate. About seven myotomes lie in front of the mouth. The anus lies against the left side of the ventral

fin where it passes into the caudal. Behind it is a region of the body of some length which does not contain any

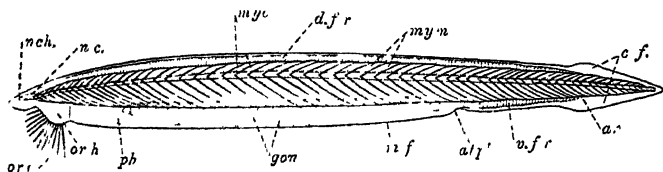


FIG. 176.—*Amphioxus*, from the left side, with the atrial floor contracted.

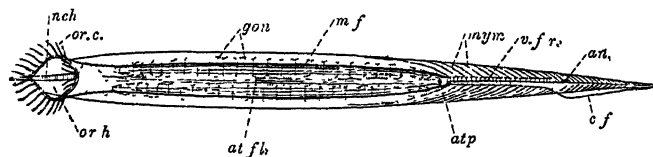


FIG. 177.—The same, from the ventral side.

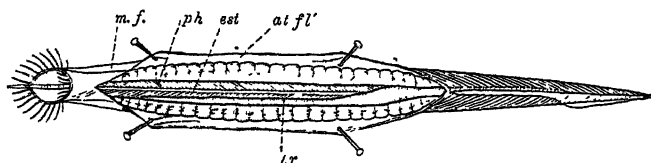


FIG. 178.—The same, from the ventral side, after the floor of the atrium has been cut open.

an., Anus; *at.fl.*, floor of atrium; *at.fl'*, the same cut through and turned back; *at.p.*, atriopore; *at.p'*, line indicating position of same in side view; *c.f.*, caudal fin; *d.f.r.*, rays of dorsal fin; *est.*, endostyle; *gon.*, gonads; *lr.*, liver; *m.f.*, metapleural fold; *mym.*, myomeres; *myc.*, myocommata or septa of connective tissue between the myomeres; *n.c.*, nerve cord; *nch.*, notochord; *or.c.*, oral cirri; *or.h.*, oral hood; *ph.*, pharynx; *v.f.r.*, rays of ventral fin.

part of the alimentary canal. Such a region is known as a *tail*. At the end of the flat region of the belly is a mid-ventral opening known as the *atriopore*, through which a current of water escapes. The mouth is below the

pointed front end in a vestibule surrounded by an *oral hood*, the edge of which is beset with slender, ciliated tentacles or *cirri*. On the inside of the hood is a lobed tract of epithelium which bears long cilia and is known as the *wheel organ*. The mouth opens through a muscular partition at the hinder side of the vestibule, known as the *velum*. The opening is bordered with about a dozen *velar tentacles*, which filter out coarse particles from the food.

The atriopore leads from a large space which lies below and at the sides of the middle part of the body and

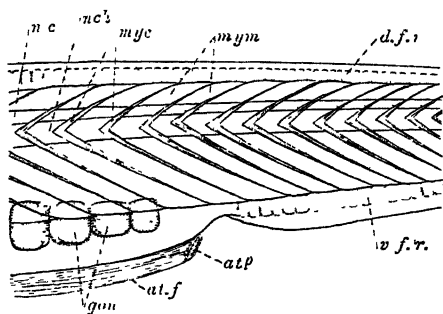


FIG. 179.—A view from the left side of the region around the atriopore of a specimen of *Amphioxus* with the atrial floor expanded. Lettering as in Figs. 176–178.

is known as the *atrium*. This space is not really within the body, but is enclosed between the body and two longitudinal folds of the body-wall, like those which form the branchiostegites of the crayfish, save that they meet in the middle line below, leaving at their hinder end an opening which is the atriopore. The atrium communicates with the pharynx by a number of slits at each side, known as the *gill slits*, separated by narrow *gill bars*, and the current of water which is passed into the mouth by the cilia around it is caused by cilia on the gill bars to flow through the slits into the atrium, and so out at the atriopore. The atrium is prolonged backwards on the right side behind the atriopore almost as far as the anus.

The skin is covered with a columnar epithelium, ciliated only within the oral hood and in parts of the atrium. The connective tissue is scanty, and consists of fibrillated ground substance with some cells. There is a thick muscular body-wall, divided, as we have seen, into segments, which are V-shaped and fit into one another so that several are cut in a transverse section. Within the body-wall lies a perivisceral coelom, not divided

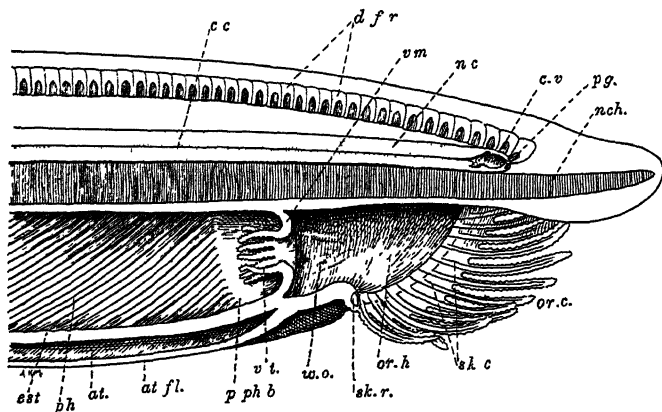


FIG. 180.—*Amphioxus*. The forepart of the body cut in half longitudinally.

at, Atrium; *at.fl.*, atrial floor; *c.c.*, central canal of nerve cord; *c.v.*, cerebral vesicle; *d.f.r.*, dorsal fin rays; *est.*, endostyle; *n.c.*, nerve cord; *nch.*, notochord; *or.c.*, oral cirri; *or.h.*, oral hood; *p.ph.b.*, peripharyngeal band; *p.g.*, anterior pigment spot; *ph.*, pharynx; *sk.c.*, skeleton of cirri; *sk.r.*, skeleton ring in oral hood; *v.t.*, velar tentacles; *v.m.*, velum; *w.o.*, part of wheel organ.

by septa, but greatly complicated by the presence of the gill slits, which reduce it in the region of the pharynx to a number of canals presently to be described. There are numerous other coelomic cavities, of which the most important are those in the region in front of the mouth, in the velum, in the metapleural folds of the larva, and in the gonads. As in the frog, the dorsal body-wall is much thicker than the ventral. In it there lies a longitudinal, hollow central nervous system, comparable to that of the frog, but at the front end not enlarged into a brain, though

the cavity, which behind is narrow like the central canal of the frog's spinal cord, is in front wide like that of the frog's brain. Below the central nervous system, along the whole length of the body, lies an elastic rod, the *notochord*, derived from the endoderm in the course of development and bound to the nerve cord by a connective tissue sheath which surrounds them both. In front it extends beyond the nerve cord. There is no skeleton of bone or cartilage, but

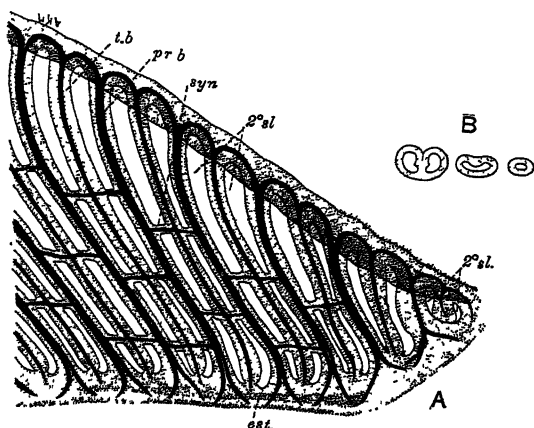


FIG. 181.—*A*, the hinder end of the pharynx of *Amphioxus*, from the left side, highly magnified; *B*, a diagram of the mode of origin of the gill clefts.

est., Endostyle; *pr.b.*, primary bar; *syn.*, synapticulæ; *t.b.*, tongue bar; *2°sl.*, the two secondary gill slits which arise from a primary slit. The skeleton is shown in black.

stiff rods of organic material support the gill bars and cirri, and gelatinous "rays" the dorsal and ventral fins.

The mouth opening leads into a wide cavity known as the pharynx, which forms about half the length of the gut, and is placed in a portion of the body which is enclosed by the atrium. Its sides are pierced by the gill slits, which lie obliquely, their lower ends being behind the upper, so that a number of them are cut in a transverse

**Alimentary
System and
Perivisceral
Cavity.**

section of the body. Each gill bar is covered with a deep columnar epithelium, ciliated except on the side towards the atrium, and contains a skeletal rod. At the tops of

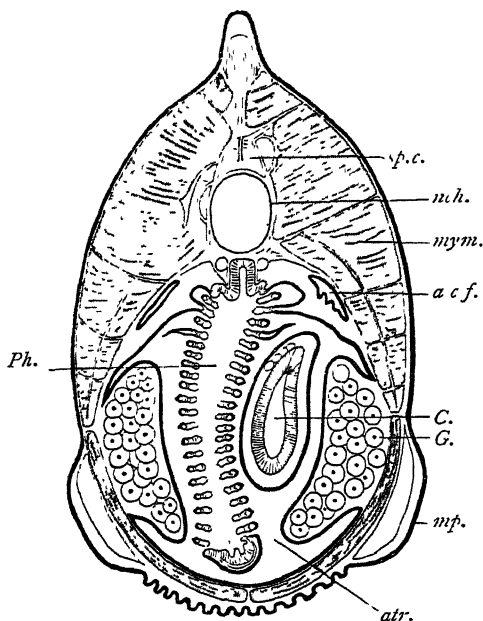


FIG. 182.—A transverse section through the pharyngeal region of *Amphioxus*.—After Ray Lankester.

sp. c., Nerve cord (spinal cord); *nch.*, notochord, beneath which lie the two suprabranchial arteries; *mym.*, myomere; *a.c.f.*, brown tube lying in dorsal coelom; *C.*, hepatic caecum; *G.*, a genital sac with ova; *mp.*, meta-pleural fold; *atr.*, atrial cavity; *Ph.*, pharynx, with dorsal and ventral grooves, and bars between gill slits. Note in the primary bars and below the ventral groove the small coelomic spaces. The ectoderm is dark throughout.

the bars these rods fork and join one another over the arches. At the lower ends the rods of alternate bars fork but do not join their neighbours, which are unsplit. The bars which contain forked rods are known as *primary bars*, the alternate bars, with unsplit rods, are *secondary bars*, or

tongue bars, because they arise in development by the down-growth of a tongue shaped process from the top of a slit, thus dividing it into two secondary openings which become the permanent slits. This process may be seen in all its stages at the hind end of the pharynx, where new slits are continually being added as long as the animal is growing.¹ The gill bars are connected by horizontal bars or *synapticulæ*, of which two or three cross each slit. These contain skeletal rods. Along the mid dorsal line of the pharynx is a deep *epibranchial groove* lined by ciliated cells. The mid-ventral wall is formed by a longitudinal bar, known as the *endostyle*, with which the lower ends of the gill bars are fused. This bears a groove lined by ciliated cells with two longitudinal bands of gland cells on each side. These cells secrete mucus which is passed forwards by the cilia. At the front end of the pharynx two *peripharyngeal bands* of long cilia connect the endostylæ with the epibranchial groove, by these bands the mucus is passed upwards to the latter, which carries it backwards to the œsophagus. In the course of this journey the mucus entangles the small organisms brought in with the water at the mouth, and carries them backwards to be digested. Each primary bar contains a narrow cœlomic canal. At the tops of the bars the cœlomic canals join a longitudinal canal, known as the *dorsal cœlom*, which lies within the body-wall above the atrium. Below the bars the canals join a longitudinal *subendostylar cœlom*. This arrangement is the remains of the originally continuous perivisceral cœlom of the pharyngeal region of the body, broken up into canals by the piercing of the walls by the gill slits. Behind the atrium, the perivisceral cœlom is a narrow but unbroken space and surrounds the alimentary canal, which runs straight back through it to the anus. The part immediately behind the pharynx is a very short, narrow œsophagus, continuous with the epibranchial groove, then comes a wider region known as the stomach. This gives off forward on its right side a pouch known as the *hepatic cœcum* or liver, which pushes before it the atrial wall and lies in the atrium beside the pharynx. Behind the stomach the gut

¹ In the larva the primary slits correspond with the myomeres, but afterwards they become more numerous

narrows and is known as the intestine. The whole alimentary canal is lined by a ciliated columnar epithelium.

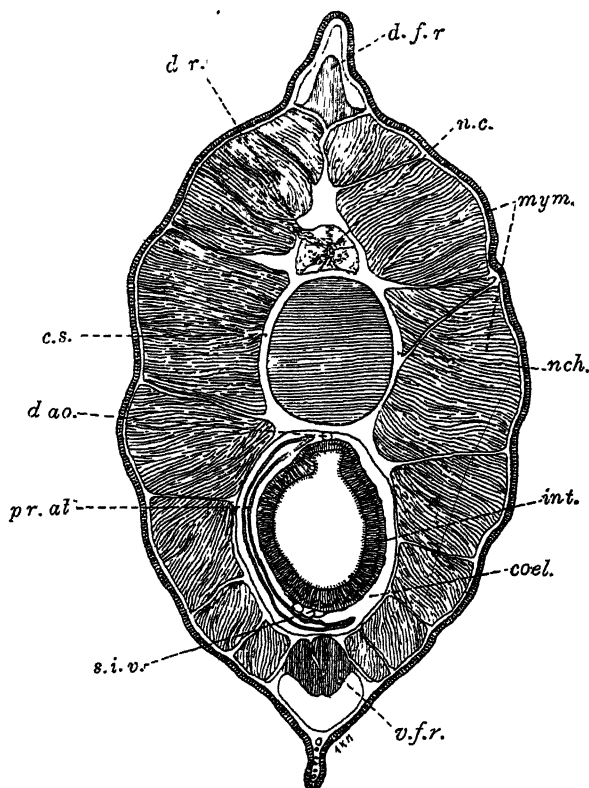


FIG. 183.—A transverse section of *Amphioxus* in the region of the intestine.

c.s., Connective tissue sheath of the notochord; *coel.*, coelom; *d.a.o.*, dorsal aorta; *d.f.r.*, dorsal fin ray, *d.r.*, dorsal root; *int.*, intestine; *mym.*, myomeres; *n.c.*, nerve cord; *nch.*, notochord, *pr.at.*, backward prolongation of the atrium; *s.i.v.*, subintestinal vein (here represented by several vessels); *v.f.r.*, ventral fin ray.

In the dorsal wall of the atrium, lying between the atrial epithelium and the dorsal coelomic canals, is a series of short tubular structures, corresponding in number

with the primary gill slits and opening into the atrium opposite the dorsal ends of the tongue bars. Each passes forwards round the top of the adjoining slit and gives off on its upper side several short branches. From each branch there projects

**Excretory
Organs.**

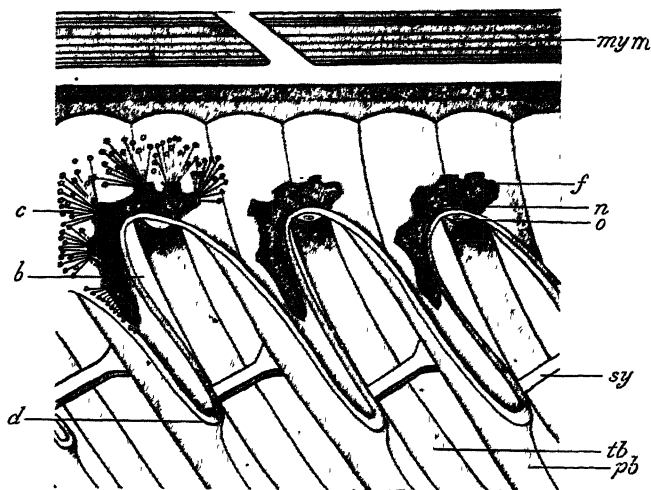


FIG. 184.—Nephridia of *Amphioxus*.—After Boveri.

A lateral view of the upper region of the pharynx, the body-wall being removed. The atrial chamber is laid completely open by the removal of its outer wall, which is cut through along its line of insertion. The result is to show that the chamber is prolonged dorsally into a series of bays (*b*), which lie outside the tongue bars (*tb*). Into these bays the nephridia (*n*) opens by pores (*o*), while they also project internally by blind funnels (*f*), fringed by very large solenocytes (*c*). The bays are separated by ridges (*d*), formed by a downgrowth of the walls of the coelom over the primary bars (*pb*); *mym.*, a myomere; *sy.*, one of the synapticulæ connecting the pharyngeal bars.

into the coelom a tuft of fibres known as *solenocytes*, which are fine, protoplasmic tubules, each ending blindly in a knob where there is a nucleus. The other end of the tubule opens into one of the branches of the main tube. Each tubule contains a long flagellum, which arises from the protoplasm round the nucleus and hangs into the main

duct. These organs are known as nephridia, although they do not, like the nephridia of the earthworm, open into the coelom. Their solenocytes recall the flame cells of the Platyhelminthes (p. 174).¹ It has been shown that if the animal be fed with carmine the colouring matter is excreted through the nephridia. A pair of funnel-shaped structures, known as *brown tubes*, which lie in the hinder part of the dorsal coelom and open into the atrium at their wide ends, have also been regarded as nephridia.

The blood is colourless and contains white corpuscles.

Vascular System.

The vascular system is closed. There is no heart, but the larger vessels are contractile and set up a circulation. A ventral or *branchial aorta* lies in the endostylar coelom and gives off to each primary gill bar a vessel which divides to take part in the formation of a rather complicated *branchial system* in the primary and secondary bars and synapticulæ. On each side the branches of this system are gathered up into a series of vessels, which open into a longitudinal *suprabranchial artery* beside the epibranchial groove, some of the blood passing through *nephridial plexuses* on the way. Behind the pharynx the suprabranchial arteries unite to form a dorsal aorta, which runs back under the notochord, giving branches to the gut and body-wall. From these blood is collected by a *subintestinal vein*, which carries it to the liver and there breaks up into a *hepatic plexus*. A hepatic vein conveys the contents of this plexus to the ventral aorta. Comparison of this circulation with that of the dogfish, presently to be described, will show that the general course of the blood is similar in the two cases. It will be seen that the direction of flow in the ventral and dorsal vessels of *Amphioxus* is opposite to that in the worm and the same as

¹ The relation between the excretory tubes of different animals is very uncertain. Those of Platyhelminthes, the earthworm, and perhaps *Amphioxus* arise in development from the ectoderm. Those of Vertebrata, Mollusca, and perhaps the crayfish arise from the mesoderm. The Malpighian tubes of insects belong to the ectodermal hind-gut. It has been proposed to restrict the term nephridia to ectodermal excretory tubes, whether they communicate with the coelom or not, and to call the mesodermal tubes *coelomoducts*. The generative ducts of the earthworm, like those of molluscs, arthropods, and vertebrates, are coelomoducts.

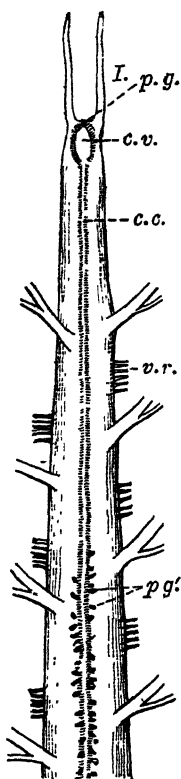


FIG. 186.—The front part of the nerve cord of *Amphioxus*, seen from above.

c.c., Central canal; *c.v.*, cerebral vesicle; *p.g.*, anterior pigment spot; *p.g.*, pigment spots in the floor of the cord; *v.r.*, ventral root—the corresponding dorsal root lies immediately behind it; *I.*, first pair of nerves.

tory pit on the dorsal surface of the left side of the body. In the adult this opening is lost, though the pit remains. The first two pairs of nerves are specialised as cerebral nerves. The first pair arise from the lower side of the anterior end of the cord, the second pair from the dorsal surface behind the cerebral vesicle. These pairs are symmetrical. They are distributed to the epidermis of the snout and are sensory in function. The remaining nerves are not symmetrical, but alternate with one another on the two sides, in correlation with the alternation of the myomeres. Each corresponds to a dorsal or a ventral root of a spinal nerve of the frog, the ventral roots being placed in front of the dorsal. The roots do not join, the ventral, which are groups of slender rootlets, passing direct to the muscles, and the dorsal, which are compact, but have no ganglia, passing in the septa between the myomeres to the epidermis. The sense organs are few and simple. Supposed tactile cells bearing short, stiff processes are scattered among the ordinary ectoderm cells, especially at the front end of the body and around the mouth. The ciliated pit already described is supposed to be olfactory. A mass of pigment which lies in the front wall of the cerebral vesicle is not sensitive to light, but small groups of pigmented organs which occur at intervals on the lower side of the canal appear to have this function.

The sexes of the lancelet are separate, but show no differences save in the nature of the gonads. **Reproductive Organs.** These are cubical bodies, twenty-six on each side, placed in the wall of the atrium, into which they shed their germs by rupture of their walls. Each corresponds to one of the myomeres and consists of a closed sac, on whose wall the germs arise. The egg is minute, but contains yolk granules. Fertilisation takes place in the water.

The lancelet is an example of a group of animals known as *Chordata* which includes also the backboneed or vertebrate animals and certain less familiar creatures. **Chordata.** Chordate animals are distinguished by the possession of a notochord, a hollow, dorsal nerve cord, and gill clefts, though in many of them some or all of these features may be present during development and lost by the adult, as the adult frog has lost the notochord and gill clefts which were possessed by the tadpole.

CHAPTER XVIII

THE DOGFISH

VARIOUS species of the small sharks known as Dogfish are found in British waters. One of the commonest of them is the Lesser Spotted Dogfish or Rough Hound, *Scyllium canicula*. Like other dogfish, it justifies its name by travelling in packs and hunting by smell. It lives usually near the sea bottom, and feeds largely upon crabs, hermit crabs, and other crustaceans, though it also often devours shell-fish, or small fishes, and will indeed take most kinds of animal food. It is very voracious and is a nuisance to fishermen by taking the bait meant for its betters. Its flesh is not unfit for food, though coarse, but it is not eaten to any great extent.

The length of a well-grown rough hound is about two feet. Its slender, sinister-looking body tapers from before backwards, and, though it shows no sudden differences in size, there may be recognised in it a head, trunk, and tail, the hinder limit of the former being marked roughly by an opening behind the eye known as the spiracle, and that of the trunk by the vent. The head is flat, and has a blunt-pointed snout, a wide, crescentic mouth on the lower side, a pair of round nostrils in front of the mouth and connected with it by *oronasal grooves*, and at the sides two slit-like eyes. Immediately behind each eye is a small, round opening, the *spiracle*, while farther back and more towards the ventral side is a row of slits which are the *gill slits or gill clefts*. The spiracle and the gill clefts open internally into the pharynx. Behind the head the body gradually changes its shape, becoming flattened from side to side instead of from above

downwards. The vent or opening of the cloaca lies in a deep longitudinal groove of the belly, just before the middle of the body. Into the same groove there opens at each side one of the *abdominal pores*, which lead from the body cavity. There are two pairs of fins and four unpaired fins. The *fore or pectoral fins*, corresponding to the arms of the frog, are a pair of flat, triangular organs attached by one angle to the sides of the ventral surface not far behind the head. The *hinder or pelvic fins* are smaller and narrower structures of somewhat the same shape, attached one on each side of the middle line of the belly in front of the vent. In the male, their inner edges are fused and there projects backwards from the under surface of each a rod, grooved along its inner side, known as a *clasper*. The unpaired fins are median structures in the tail. Two, known as the anterior and posterior *dorsal fins*, are on the back, one, the *ventral fin*, is on the under side, and another, the *caudal fin*, surrounds the end of the tail. This fin has two lobes, and the axis of the tail is turned upwards and passes into the upper lobe.

Certain generalisations which we have made in the course of the previous chapters enable us to state in a few words a good deal of information about the anatomy of the dogfish. A

**General
Internal
Features.**

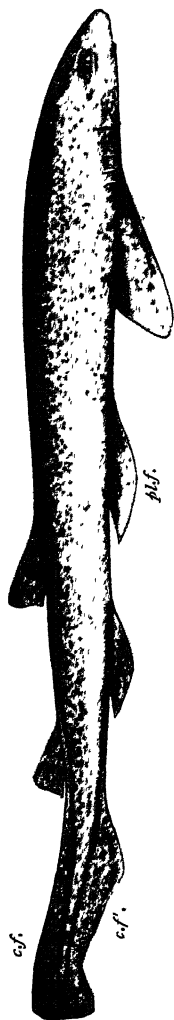


FIG. 187.—The Rough Hound.

Note mouth, eye, spiracle, lateral line, gill clefts, pectoral and pelvic fins, dorsal fins, caudal fin, ventral fin between caudal and pelvic fins.

c.f., Upper lobe of caudal fin; *c.f.*, lower lobe of the same; *p.f.*, pelvic fin.

dogfish is a metazoan animal. It is triploblastic and coelomate. It has a large, coelomic, perivisceral cavity and a closed circulation. It is bilaterally symmetrical. It is segmented, though the primary segmentation is best seen in the early stages of development, and is represented in the adult only by the arrangement of the muscles of the body-wall, the segmentation which is found in the backbone and nervous system arising later. It is chordate. Lastly, like

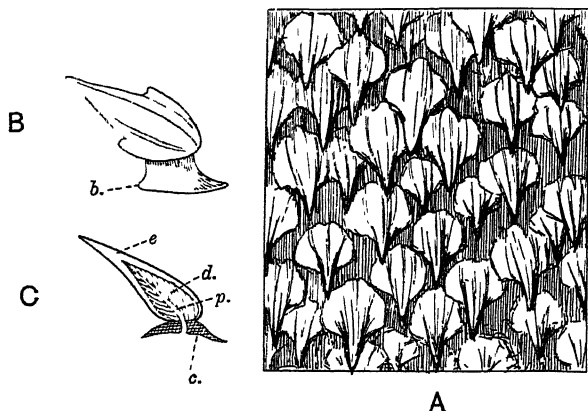


FIG. 188.—Placoid scales.

A, A portion of the skin of the rough hound as seen under a hand lens; *B*, a single scale removed from the skin; *C*, the same in section (diagrammatic).

b., Base of the scale; *c.*, the same in section; *d.*, dentine; *e*, enamel; *p.*, pulp cavity.

the frog, it is a *backboned or vertebrate* animal. This term implies more than the possession of a backbone. The *Vertebrata* are a large group of animals which have in common, besides the features we have just mentioned, the following: (1) they possess an internal skeleton of bone or cartilage, part of which forms a skull and backbone; (2) their central nervous system, which is hollow and dorsal like that of all chordate animals, consists of a spinal cord and a complicated brain; (3) the gill clefts, which they all possess during some period of development, are few and

do not open into an atrium ; (4) they have a heart, which lies below the gut ; (5) most, though not all of them, possess two pairs of limbs and none have more.

Upon the back and sides of the rough hound the skin is of a grey-brown colour with small spots of darker brown ; upon the belly it is whitish. It feels smooth to the hand if it be stroked from head to tail, but rough if it be stroked in the opposite direction. This is due to the presence of *scales*, which are not flat like those of most fishes, but bear minute spines directed backwards.

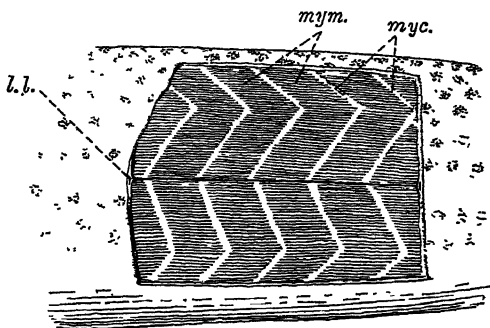


FIG. 189.—Part of the tail of a dogfish seen from the left side, with a piece of the skin removed.

l.l., Tube of the lateral line ; *myc.*, myocommata or septa of connective tissue ,
mym , myomeres

Such scales are said to be *placoid*. Each consists of a calcified basal plate embedded in the dermis, and a spine which is composed of dentine covered with enamel. A pulp cavity, containing highly vascular connective tissue, passes through the base into the spine. It will be seen that the general features of such a scale resemble those of the tooth of a frog. In fact the teeth of the dogfish, though they are larger, have the structure of the scales, and we must regard teeth as modified scales.

The muscles of the body-wall are for the most part segmentally arranged, each muscle-segment being known as a *myomere*. The myomeres do not lie straight, but

each is bent four times, so that it runs a zigzag course from the middle of the back to that of the belly.

Muscles and Movements. In the muscles of the head, throat, and fins the segmental arrangement is not apparent. The myomeres are separated by partitions of connective tissue, between which their fibres run longitudinally. By the action of these muscles, especially in the powerful tail, which is more than half the length of the body, the animal is driven through the water, the tail working from side to side with a twisting motion, as an oar may be used from the stern of a boat to propel it. The upturned position of the axis of the tail helps to keep the snout upon the ground as the fish "noses" about for its food. The dorsal and ventral fins act like the keel of a boat in keeping the body upright, and the paired fins help in balancing and are used in steering upwards and downwards.

The scales of the dogfish constitute a part of the skeleton known as the *exoskeleton*, which in the frog is represented only by the teeth.

Skeleton : General Features. The *endoskeleton* of the dogfish corresponds to that of the frog in its main outlines, but differs from it in some important respects. (1) It is wholly cartilaginous, like that of the tadpole, containing nothing which corresponds either to the membrane bones or to the cartilage bones of the frog, though in places the cartilage is calcified. (2) The axial skeleton is traversed below the central nervous system by a peculiar rod, the notochord, which consists of large, vacuolated cells with stout walls, and is derived from the endoderm in the course of development. This is present in the tadpole, but in the adult frog is represented only by pads of tissue between the centra of the vertebræ. (3) There are no structures which represent any part of the sternum. (4) In correspondence with the difference in the shape of the limbs, their skeleton differs entirely in the two animals. (5) Unlike that of the tadpole, the median fins are supported by rays.

The backbone consists of about 130 vertebræ, in each of which the centrum is pierced from end to end by a canal for the notochord. This canal is narrower in the middle of the vertebra, so that the notochord is constricted, and after its removal

the centrum appears as a biconcave disc. On each side the centrum bears a pair of *ventrilateral processes*.¹ In the trunk region these are directed outwards and bear short *ribs*, which lie beneath the muscles of the back; in the hinder part of the body the processes are directed downwards and are known as *hæmal arches*, enclosing a *hæmal canal*, in which lie the caudal artery and vein. Towards the hinder end of the tail they fuse at their ends and bear a median *hæmal spine*. Between the neural arches of successive vertebræ are wide gaps which are closed by *intercalary pieces*. The *neural spines* are a series of flat median pieces of cartilage, twice as numerous as the vertebræ, which fill the gaps between the tops of the neural arches and intercalary pieces and roof in the vertebral canal.

The skull consists, like that of the frog, of a cranium which contains the brain, with a pair of nasal capsules in front, a pair of auditory capsules one at each side of the hinder end, and a visceral skeleton below. The nasal capsules are large, thin-walled, cartilaginous structures, continuous with the cranium, widely open below, and separated by an *internasal septum* or *mesethmoid cartilage*. Three slender processes, one from the front wall of each capsule and one from the mesethmoid cartilage, project into the snout and are together known as the *rostrum*. At the junction of the cranium and the nasal capsules the roof of the skull shows a large gap, the *anterior fontanelle*. From the sides of the cranium large *supra- and suborbital ridges* project to protect the orbit above and below. On the auditory capsules, which are continuous with the cranium, ridges mark the position of the semi-circular canals. A median depression on the roof between the auditory capsules communicates on each side with a canal, the *aqueductus vestibuli*, which leads to the internal ear and puts the endolymph into communication with the sea water through a small opening. There is no ear drum. At the hinder end, between two occipital condyles, may be seen the notochord, which passes into the floor of the cranium for some distance. Numerous openings pierce the wall of the

¹ These are often called transverse processes, but they do not correspond with those of the frog, which belong to the neural arches.

cranium. (1) On the roof lies the anterior fontanelle which we have already mentioned. (2) At the front end two large foramina put the cranial cavity in continuity with those of the nasal capsules. Through these the olfactory nerves pass from the surface of each olfactory lobe of the brain into the olfactory organ. (3) On each side wall numerous openings allow the passage of nerves and blood vessels to and from the orbit. The relative sizes and positions of these are seen in Fig. 190. (4) Just behind the auditory capsules, at the bottom of a deep pit, is the foramen for the ninth nerve, and on each side of the occipital condyles is a foramen for the passage of the tenth nerve. (5) On the under side there may be seen two shallow grooves, along which the internal carotid arteries run. Where these meet there is a small opening, through which the two arteries enter the cranium. At the outer ends of the grooves are the openings through which the external carotid arteries pass from the roof of the mouth to the orbits. (6) At the hinder end of the skull is the large foramen magnum. The *visceral skeleton* is a series of seven arches, each consisting of several pieces, which lie at the sides of the mouth. The first of these is the *mandibular arch*, which forms the skeleton of the jaws. Each half of the *upper jaw-bar or palato-pterygo-quadrate cartilage* is a rod which meets its fellow in front of the mouth and is there joined to it by a ligament. It is attached to the cranium in front of the orbit by the *ethmopalatine ligament* and behind to the auditory capsule by a *postspiracular ligament*. Each half of the lower jaw is formed by Meckel's cartilage, which is a wide, flat bar, tapering forwards to a point, where it is joined with its fellow by a ligament. It articulates behind with the palato-pterygo-quadrate cartilage and is joined by ligament to the hyomandibular cartilage which forms its principal attachment to the skull. The second or *hyoid arch* consists of two pieces, an upper *hyomandibular cartilage*, which is a short, stout rod articulated with a large facet on the side of the auditory capsule, and a longer, more slender, *ceratohyal cartilage*, which passes forwards and inwards from the hyomandibular to join a median plate, the *basihyal cartilage*, in the floor of the mouth. The remaining five arches are the *branchial arches*.

Each branchial arch contains above a flat, pointed *pharyngobranchial* which, starting beside the backbone, slopes forwards to join an *epibranchial*, which lies at the side of the pharynx in a line with the hyomandibular cartilage. From the lower end of this the *ceratobranchial* runs forwards and inwards parallel with the ceratohyal and mandibular cartilages. The first four ceratobranchials are connected with *hypobranchials* in the floor of the pharynx. The first hypobranchial is small and joins the first ceratobranchial with the basihyal;

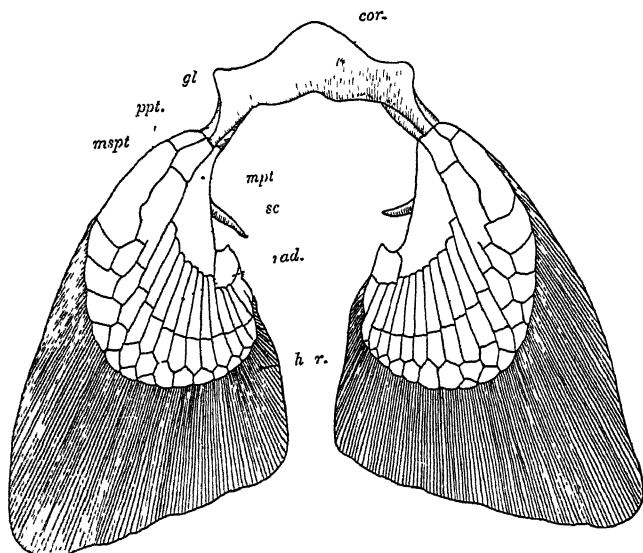


FIG. 191.—The skeleton of the pectoral fins and girdle of a dogfish, seen from the ventral side.

cor., Coracoid region; *gl.*, glenoid surface; *h. r.*, horny rays; *mpt.*, metapterygium; *mspt.*, mesopterygium; *ppt.*, propterygium; *rad.*, cartilaginous rays; *sc.*, scapula.

the three hinder are larger and directed backwards and inwards. The last two pairs of hypobranchials and the fifth ceratobranchials join a median *basibranchial plate*. The epibranchial, ceratobranchial, hyomandibular, and ceratohyal cartilages bear *gill rays* along their hinder borders. Outside the upper and lower jaws lie a pair of *labial cartilages*, and along the outer sides of the second, third, and fourth ceratobranchials are *extrabranchials*.

The median fins are supported by a skeleton consisting of several series of rays. The series nearest the body are cartilaginous rods known

as *basalia* and are attached to the neural and hæmal spines. They are succeeded by a similar series known as *radialia*, and these by two rows of small polygonal plates of cartilage which support a final series of horny rays or *actinotrichia*. In the caudal fin the cartilaginous rays are not distinct from the neural and hæmal spines.

The limbs are anchored into the body by girdles which correspond to

Limbs. those

of the

frog. The pec-

toral girdle con-

sists of two

curved pieces of

cartilage at the

sides of the body,

of which the

lower ends are

fused in the mid-

ventral line. To

the hinder sides

of these pieces

are articulated

the fins. The

surface of articu-

lation is the

glenoid facet, the

portion of the

girdle above the

facet being the

scapular region

and that below

the *coracoid*. The

scapula is rod-like; the coracoid is broad and flat and

supports the floor of the pericardium. The pectoral fin

articulates with its girdle by three basal cartilages, the *pro-*

meso-, and *metapterygia*, of which the former is the anterior

and smallest, the metapterygium the hinder and largest.

Along the outer borders of these pieces are set a series of

radialia. The pro- and mesopterygia each bear one stout

ray, the metapterygium several, which are slender. To the

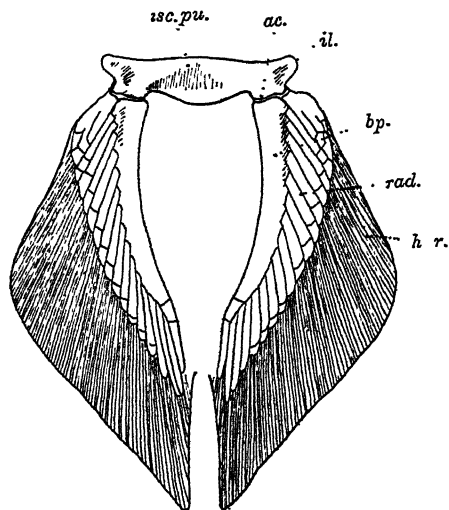


FIG. 192.—The skeleton of the pelvic fins and girdle of a female dogfish.

ac., Acetabular surface; bp., basipterygium, h.r., horny rays; il., iliac process; isc.pu., ischio-pubic region; rad., cartilaginous rays.

ends of these, smaller, polygonal pieces are attached, and to

them in turn horny *actinotrichia*. The pelvic girdle is a stout, straight bar of cartilage placed athwart the belly and bearing a blunt knob at each end. The main part of the bar is the *ischio pubic region*, the knobs are the *iliac processes*, and the fins articulate with an *acetabular facet* upon the hinder border at the base of the iliac processes. The fin has a long, inwardly-curved *basipterygium*, bearing a row of radialis along its outer side. In the male it also bears a long piece of cartilage which supports the clasper.

The perivisceral cavity lies wholly in the trunk, and is divided into two parts, the small pericardium just in front of the pectoral fins, and the large abdominal or peritoneal cavity behind it, between the two pairs of fins. The two cavities are divided by a membranous septum, but a narrow passage, the *pericardio-peritoneal canal*, leads from one to the other below the cesophagus. As in the frog, the abdominal cavity contains among other organs the whole of the alimentary canal with the exception of the mouth and pharynx. The gape of the mouth is edged with several rows of teeth, which, as we have seen, are simply enlarged scales. These lie in a part of the skin which passes over the jaw and is tucked into a groove within it. They are not in any way attached to the jaw. As they wear away, they are replaced by new rows which are constantly being formed in the groove and carried up over the edge of the jaw by the growth of the skin. The pharynx is only distinguished from the mouth by possessing the inner openings of the spiracle and gill clefts. These are placed between the arches of the visceral skeleton, the first gill cleft lying between the hyoid and first branchial arches. The clefts do not pass straight outwards through the wall of the throat, but the outer opening of each is at some distance behind the inner, so that the cleft is a pouch which slants backwards and outwards from the pharynx to the exterior. The pouches are spacious cavities, being deep, and considerably taller than their openings at either end, though the inner opening is larger than the outer. On each wall of the pouch lie a number of folds which constitute a *gill*. These are highly vascular, and in fresh specimens have consequently a bright red colour. There is

**Cœlom and
Alimentary
System.**

a gill on each side of each cleft except the last, which has no gill on the hinder side. The spiracle is a small cleft of the same series as the gill cleft, and bears on its front side a vestige

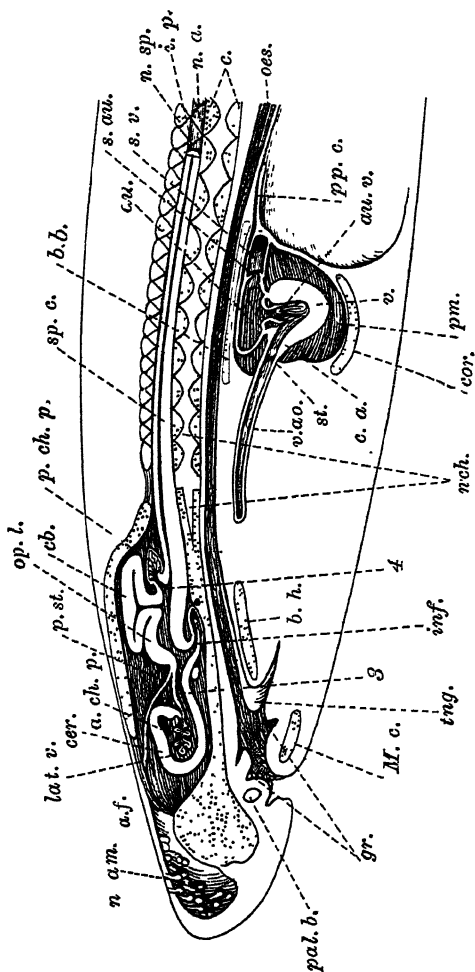
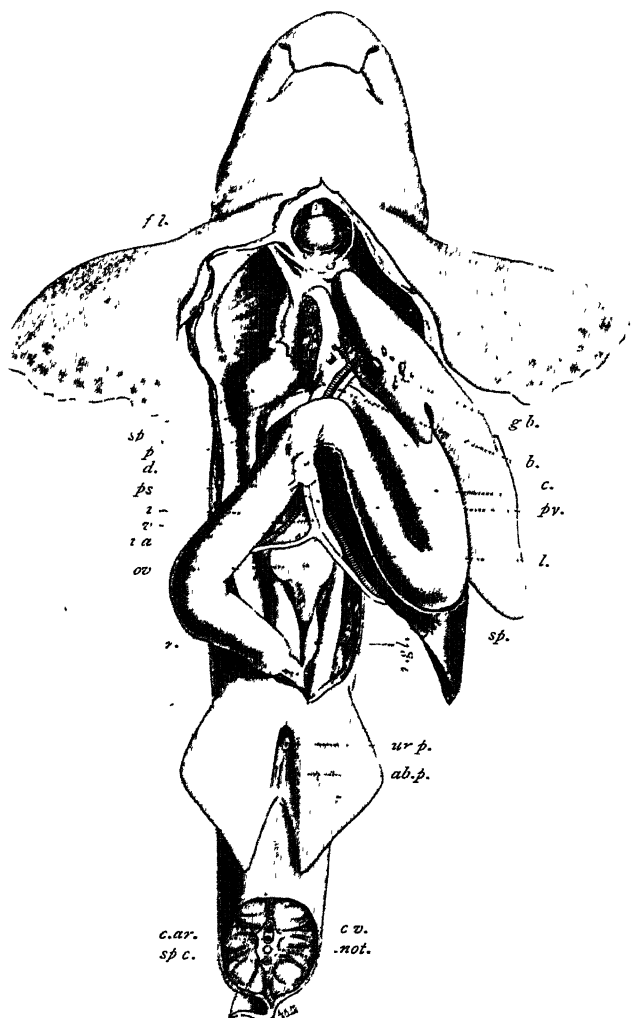


FIG. 193.—A semi-diagrammatic drawing of a longitudinal section through a dogfish, passing slightly to the right of the middle line.

a.ch.p., Anterior choroid plexus; *a.f.*, anterior fontanelle; *an.*, auricle; *an.v.*, auriculo-ventricular opening and valve; *b.b.*, basibranchial cartilage; *b.h.*, basihyal cartilage; *c.*, centrum; *c.a.*, conus arteriosus; *cb.*, cerebellum; *cer.*, cerebrum; *cor.*, coracoid region of the pectoral girdle; *gr.*, grooves in which the teeth are formed; *i.p.*, intercalary plate; *inf.*, infundibulum; *lat.v.*, lateral ventricle; *M.c.*, Meckel's cartilage; *n.a.*, neural arch; *n.a.m.*, ampullary sense organ; *n.sp.*, neural spine; *nch.*, notochord; *oes.*, esophagus; *op.l.*, optic lobe; *p.ch.p.*, posterior choroid plexus; *p.st.*, pineal stalk; *pal.b.*, palatine bar; *pm.*, pericardium; *pp.c.*, pericardio-peritoneal canal; *s.v.*, sinus venosus; *sp.c.*, spinal cord; *st.*, semilunar valves; *tng.*, tongue; *v.*, ventricle; *v.a.o.*, ventral aorta; 3, third ventricle; 4, fourth ventricle.



For legend see opposite page.

of a gill, known as a *pseudobranch*. The regions between the clefts, and those immediately in front of the first cleft (the spiracle) and behind the last, are known as *visceral arches*. Each, as we have seen, contains a skeletal arch. We shall see later that it also contains an artery and a nerve. The spiracle lies between the mandibular and hyoid arches. The gills are respiratory organs. In life the fish is continually taking in water at the mouth and passing it out over the gills and through the clefts by a munching action of the lower jaw. From the pharynx the narrower oesophagus leads back through the coelom to the stomach. This is sharply divided into a cardiac and a pyloric part. The former is a sac, in shape not unlike the stomach of the frog, near its hinder end on the right side arises the narrow tubular pyloric division, which runs forwards beside the cardiac. At its front end a slight constriction marks the presence of the pyloric sphincter and divides it from the intestine. The main part of this is a long, wide sac, known as the ileum, which passes backwards towards the cloaca and has its internal surface increased by a spiral fold of the mucous membrane known as the *spiral valve*. Between this region and the pyloric sphincter lies a short, somewhat narrower region called the duodenum or *bursa entiana*, which is without a spiral valve and receives the ducts of

FIG 194.—A female dogfish in which the abdominal and pericardial cavities have been opened from the ventral side, and the viscera somewhat displaced. The pericardium has been opened slightly to the left of the middle line, and the right lobe of the liver has been cut away.

ab p, Abdominal pores; *b*, bile duct; *c*, cardiac limb of stomach; *car*, caudal artery; *cv*, caudal vein; *d*, bursa entiana; *fl*, falciform ligament, with the internal opening of oviducts; *gb*, portion of gall bladder appearing on surface of left lobe of liver in which it is embedded; *i*, intestine; *ia*, intestinal branch of anterior mesenteric artery; *l*, lienogastric artery; *not*, notochord; *ov*, ovary; *p*, portal vein lying beside hepatic artery; *ps*, pancreas with duct opening into intestine; *py*, pyloric limb of stomach; *r*, rectum between hinder ends of oviducts, with rectal gland (*rgl*) attached to its dorsal side; *sh*, right shell gland on course of right oviduct; *sp*, spleen; *sp c*, spinal cord; *ur p*, urinary papilla; *v*, branch of portal vein formed by junction of intestinal and splenic veins.

Besides the above note—nostrils, oronasal grooves, mouth, pectoral and pelvic fins, pericardial and abdominal cavities, heart, consisting of sinus venosus (behind), ventricle, auricle (showing at sides of ventricle) and conus cloacae and transverse section of tail showing at the sides the myomeres, above the anterior dorsal fin, and in the middle the cartilage of the backbone enclosing spinal cord, notochord and blood vessels.

the liver and pancreas. At its hinder end the ileum narrows and loses its spiral valve, thus becoming the rectum, this in turn ending in the wider cloaca, which receives the urinary and generative ducts and opens by the vent. There is no bladder. The liver is a very large organ, consisting of long right and left lobes united in front and slung by the *falciform ligament* from the anterior wall of the peritoneal cavity. The gall bladder is embedded in the front part of the left lobe of the liver, but usually a part of it shows upon the surface. From it the bile duct runs backwards to open into the intestine, lying in the membrane or *omentum* which carries the hepatic artery and portal vein. The pancreas lies between the stomach and intestine; it is long and narrow and has in front a rounded ventral lobe, from which its duct passes to the ventral side of the intestine. The *rectal gland* is a small cylindrical structure which opens into the dorsal side of the rectum by a duct. The spleen must be mentioned here, although it has no connection with the alimentary canal. It is attached by membrane to the hinder end of the stomach as



FIG. 195.—Spiral valve.
—After T. J. Parker.

to the hinder end of the stomach as a triangular lobe with a forward prolongation along the right side of the pyloric division.

The kidneys of the dogfish are relatively longer than those of the frog, but otherwise resemble them in position and structure, lying above the abdominal cavity just outside the peritoneum, and consisting of numerous tubules, whose nephrostomes in this case remain open. In the early stages of development the tubules correspond with the muscle segments, but later they become numerous. The kidneys have three sections, known as the *fore*, *mid*, and *hind kidneys*, or *pro*-, *meso*-, and *metanephros*, but the first of these is rudimentary and disappears early in development. The mesonephros is a long, narrow organ which in the adult female is reduced to a mere vestige and can

**Excretory and
Generative
Organs.**

only be found by removing the peritoneum, but in the male is better developed and, with its duct, makes a ridge along the body cavity. The metanephros is a larger organ which forms a cushion-like swelling and is the principal excretory organ in both sexes; it is not seen in the frog, where the whole kidney is mesonephric. A duct, known as the *mesonephric* or *Wolffian duct*, corresponding to the kidney duct of the frog, runs the whole length of the kidney, lying upon its ventral face and receiving the tubules of the mesonephros. In the female it is straight and its hinder end is widened to form a *urinary sinus*, which joins its fellow to open into the cloaca upon a *median urinary papilla*; in the

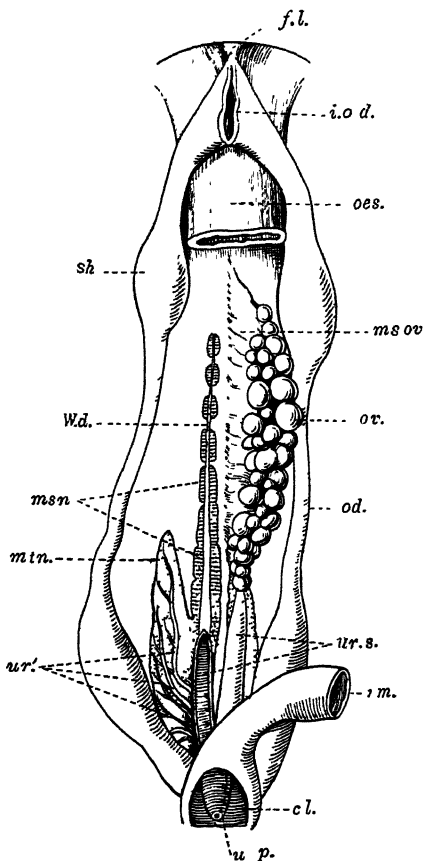


FIG. 196.—The reproductive organs of a female dogfish.

cl., Cloaca; *f.l.*, part of the "falciform" ligament; *i.o.d.*, internal opening of the oviducts; *msn.*, mesonephros; *ms ov.*, mesovarium; *mn.*, metanephros; *od.*, oviduct; *oes.*, cesophagus; *ov.*, ovary; *r.m.*, rectum; *sh.*, shell gland; *ur.*, ducts of metanephros; *u p.*, urinary papilla; *ur.s.*, urinary sinus; *W.d.*, Wolffian duct.

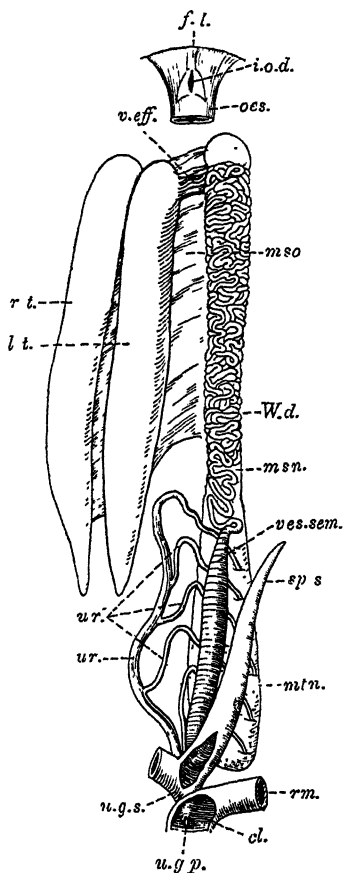


FIG. 197.—The reproductive organs of a male dogfish.

cl., Cloaca; *f.l.*, "falciform" ligament; *i.o.d.*, rudiment of the internal opening of the oviducts; *l.t.*, left testis; *msn.*, mesonephros; *mso.*, mesorchium; *mtn.*, metanephros; *oes.*, oesophagus; *r.t.*, right testis; *r.m.*, rectum; *sp.s.*, sperm sac; *u.g.p.*, urinogenital papilla; *u.g.s.*, urinogenital sinus; *u.r.*, ureter; *u.r.*, ducts of metanephros; *v.eff.*, vasa efferentia; *ves.sem.*, vesicula seminalis; *W.d.*, Wolffian duct or vas deferens.

male it is coiled and serves, as in the frog, as the vas deferens, its swollen hinder part being a vesicula seminalis. The tubules of each metanephros are collected into five or six ducts, which in the female open into the urinary sinus of its side, but in the male join to form a *ureter* which passes backwards to open separately from the vesicula seminalis into a median *urinogenital sinus*. This has two forward horns known as the *sperm sacs*, which lie upon the ventral faces of the vesiculæ seminales, and opens behind into the cloaca by a *urinogenital papilla* behind the anus. There is a single ovary, which probably represents that of the right side of the frog. It hangs into the body cavity and varies in size and appearance with age. The ova are in different stages of ripeness, the ripest being very large and yolky. They are shed into the body cavity and passed forwards by contractions of the abdominal walls to the front of the peritoneal space, where they enter the *internal opening*

of the oviducts. The latter are large, straight tubes, one on each side of the body, attached to the dorsal wall of the coelom. They start from a common opening in the falciform ligament, not far behind which each has a round swelling known as the *shell gland*. At the hinder end of the trunk they enter the cloaca by a common opening just behind the anus. The testes

are a pair of long organs slung by membranes from the dorsal wall of the coelom. Each communicates at its front end with the mesonephros of its side by several small vasa efferentia, the sperm passing through these into the mesonephric tubules and thence to the vas deferens or Wolffian duct, by which it is conveyed to the urinogenital sinus. A rudiment of the internal opening of the oviducts is found in the falciform ligament of the male. Sperm is passed by the aid of the claspers into the cloaca of the female and fertilisation takes place within her. The eggs are laid in flat, oblong, brown shells whose angles are prolonged into tapering tendrils, which twine round seaweeds and thus anchor the egg. Protected by the shell, the young dogfish develops slowly at the expense of the yolk, which comes to be contained in a sac attached to its belly. At one stage long, vascular threads project from the gill clefts of the little fish. These are the so-called external gills, but they are covered with endoderm and thus differ from the true external gills of the tadpole.

The heart of a dogfish lies in the pericardium between

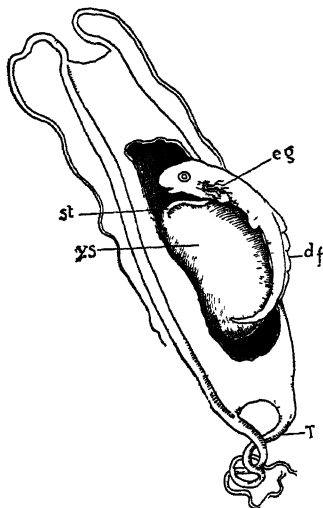


FIG. 198.—An embryo dogfish in its egg-case ("mermaid's purse") which has been cut open to show the contents.—From Thomson.

d.f., Dorsal fin fold; *e.g.*, "external" gills; *st.*, stalk of yolk-sac; *T.*, tendrils, prolongations of egg-case by means of which it is moored to seaweed; *y.s.*, yolk-sac.

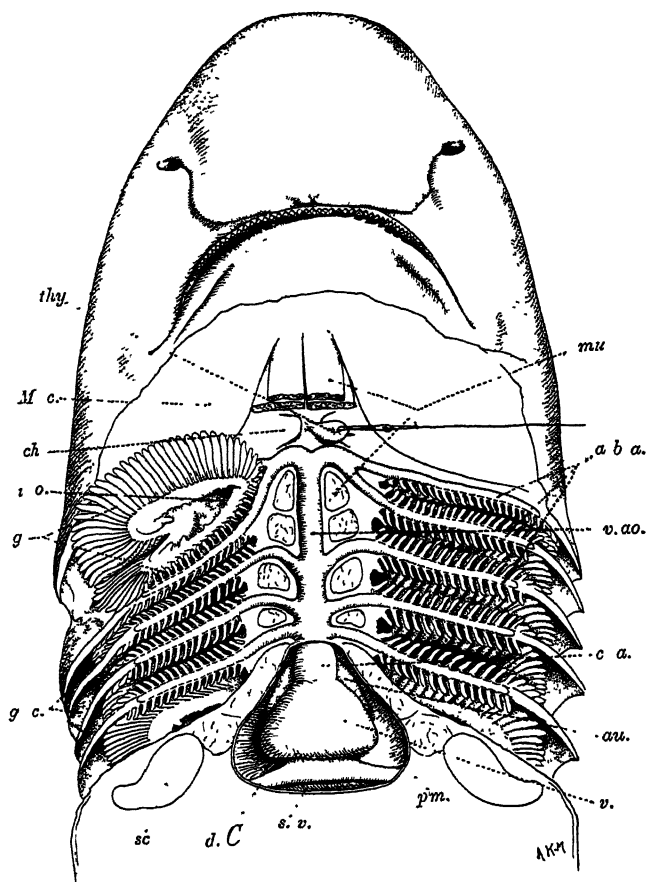


FIG. 199.—The forepart of the body of a dogfish, dissected to show the heart and ventral arterial system.

a.b.a., Afferent branchial arteries; *au.*, auricle; *c.a.*, conus arteriosus; *ch.*, ceratohyal cartilage; *d.C.*, ductus Cuvieri; *g.*, gills; *g.c.*, gill clefts; *i.o.*, internal opening of the first gill cleft; *M.c.*, Meckel's cartilage; *mu.*, muscles from coracoid region of shoulder girdle to various parts of visceral skeleton; *p.m.*, pericardium; *s.v.*, sinus venosus; *sc.*, scapula; *thy.*, thyroid gland (displaced); *v.*, ventricle; *v.a.*, ventral aorta.

the hinder gill clefts It is a median structure with muscular walls, and consists essentially of an irregular tube, bent like an S (Fig 193) and composed of four successive chambers The hindermost chamber is the thin walled, triangular sinus venosus, which lies with its base against the hinder wall of the pericardium In front of it comes the thicker walled auricle or atrium This is also triangular, with its apex forwards, and has its hinder angles widened into pouches, but is not divided into two chambers like that of the frog The S then curves downwards, as the very thick walled, conical ventricle, which lies below and somewhat behind the auricle From it the narrow conus arteriosus passes forwards through the front wall of the pericardium to become the ventral aorta, which is merely the foremost part of the single vessel whose thickening and twisting produces the heart behind The heart contracts from behind forwards, and drives blood into the ventral aorta, reflux being prevented by a valve at the opening of the sinus into the auricle, another at the auriculo-ventricular opening, and two rows of semilunar or watch-pocket valves in the conus

The ventral aorta lies in the middle of the throat below the pharynx and between the gill clefts, giving off *afferent branchial arteries* to the fourth, third, and second branchial arches, and ending by dividing into two vessels, each of which again forks to supply the first branchial and hyoid arches of its side There are thus five afferent branchial arteries These, together with the ventral aorta, form the *ventral arterial system* The thyroid gland, an organ of doubtful function (p 50) which does not belong to the vascular system, lies below the anterior end of the ventral aorta as a pear shaped body with the stalk forwards From the afferent branchial arteries the blood passes into the capillaries of the gills, where it is oxygenated and gathered up into *efferent branchial arteries* These form a complete loop round each of the first four clefts, the loops being joined fore and aft by short horizontal vessels at about the middle of their lengths The last cleft, having no gill on its hinder side, has an efferent vessel on its front side only, and all the blood of this vessel passes by the horizontal vessel into that of the gill in front From the dorsal end

Blood Vessels
Heart

Arteries

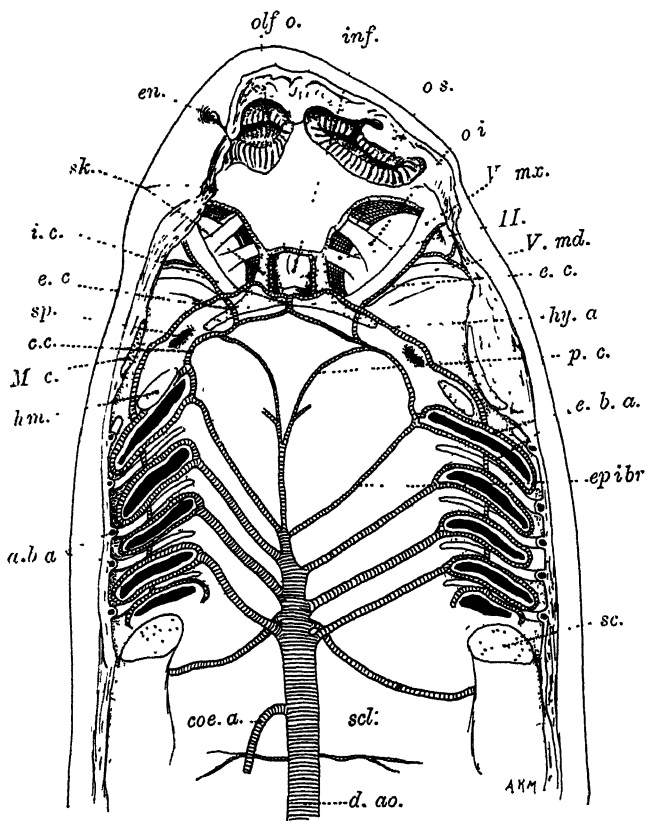


FIG. 200.—The forepart of a dogfish, dissected from the ventral side, to show the dorsal arterial system, the olfactory organs, and certain structures in the orbits. The middle part of the floor of the mouth has been removed.

a. b. a., Afferent branchial arteries; *c. c.*, common carotid artery; *coe. a.*, coeliac artery; *d. ao.*, dorsal aorta; *e. b. a.*, efferent branchial arteries; *e. c.*, external carotid; *en.*, nostril; *epibr.*, epibranchial artery; *hm.*, hyomandibular cartilage; *hy. a.*, hyoidean artery; *i. c.*, internal carotid arteries; *inf.*, infundibulum; *M. c.*, Meckel's cartilage in lower jaw; *o. i.*, inferior oblique muscle; *o. s.*, superior oblique muscle; *olf o.*, olfactory organ; *p. c.*, posterior carotid artery; *sc.*, scapula; *scl.*, subclavian artery; *sk.*, skull; *sp.*, spiracle; *V. md.*, *V. mx.*, mandibular and maxillary branches of fifth nerve; *II.*, optic nerve.

of each of the complete loops arises a vessel known as an *epibranchial artery*, which runs backwards and inwards on the roof of the pharynx to join the median dorsal aorta opposite to its fellow of the other side. From the dorsal end of the first efferent branchial artery, just outside the origin of the first epibranchial artery, arises the common carotid artery. This runs forwards and inwards under the skull. Behind the orbit it divides into an external and an internal branch. The former immediately passes through the opening we have mentioned (p. 283) and runs forwards along the floor of the orbit to supply the upper jaw and the

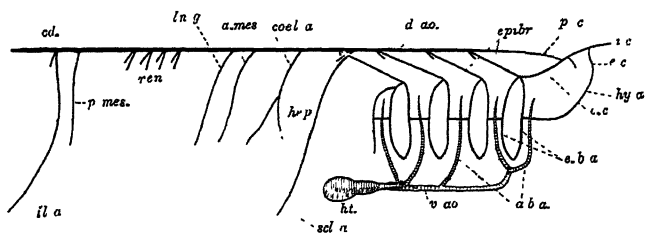


FIG. 201.—A diagram of the arterial system of a dogfish, seen from the right side.

a.b.a., Afferent branchial arteries; *a.mes.*, anterior mesenteric artery; *c.c.*, common carotid artery; *cd.*, caudal artery; *coel.a.*, coeliac artery; *d.ao.*, dorsal aorta; *e.b.a.*, efferent branchial arteries; *e.c.*, external carotid artery; *epibr.*, epibranchial arteries; *h.t.*, heart; *h.p.*, hepatic artery; *hy.a.*, hyoidean artery (this joins the internal carotid of the opposite side, which is not shown); *i.c.*, internal carotid artery; *il.a.*, iliac artery; *ln.g.*, lienogastric artery; *p.c.*, posterior carotid artery; *p.mes.*, posterior mesenteric artery; *ren.*, renal arteries; *scl.a.*, subclavian artery; *v.ao.*, ventral aorta.

snout. The internal carotid artery continues its course in the carotid groove, towards the middle line, where with its fellow it passes through the internal carotid foramen into the cranium to supply the brain. Outside the carotid yet another artery arises from the first efferent branchial vessel. This is the *hyoidean artery*, which starts in a line with the horizontal vessels which join the loops, runs forwards to the spiracle, where it supplies the pseudobranch, crosses the orbital floor, enters the cranium by a small foramen in the inner wall of the orbit, and joins the crossed internal carotid artery of the opposite side. The dorsal aorta ends in front by breaking into two small *posterior carotid arteries*, which

curve outwards and join the common carotid trunks. Just before it is joined by the last pair of epibranchial vessels it gives off a pair of subclavian arteries, which run backwards and outwards to the fore fins. Behind the pharynx it runs backwards along the whole length of the body below the backbone, lying, in the tail, in the hæmal canal as the *caudal artery*. Besides paired vessels to the body-wall, it gives off to the viscera several median vessels, known successively as the cœliac (of which the hepatic is a branch), anterior mesenteric (of which the genital is a branch), lienogastric, and posterior mesenteric, and to the kidneys several paired renal arteries.

The sinus venosus receives the whole of the blood returning to the heart, by a number of very large veins which are called *sinuses*, though, unlike the sinuses of the crayfish, they do not take the place of capillaries as well as veins in the circulation, but are merely enlarged parts of the veins. The blood from the liver returns direct to the sinus venosus by two *hepatic sinuses* which enter its hinder side. The rest of the blood is returned by two large vessels known as *ductus Cuvieri* which join the sinus venosus, one on each side in the pericardium. Into these the blood from the region of the body in front of the fore-fins is conveyed by a pair of large dorsal *anterior cardinal sinuses* and two smaller *inferior jugular sinuses* below the throat. Each anterior cardinal sinus communicates in front with an *orbital sinus* around the eye, and this in turn with a *nasal sinus* around the olfactory organ. A *hyoidean sinus* in the hyoid arch joins the anterior cardinal and inferior jugular sinuses. At the outer end of each ductus Cuvieri a *subclavian sinus* enters from the arm. On its hinder side a very large *posterior cardinal sinus* brings back blood from the trunk. The two posterior cardinal sinuses converge backwards, growing narrower, and lie side by side between the kidneys, from which blood passes into them by numerous renal veins. Blood from the tail is returned by the *caudal vein*; this divides opposite the hinder ends of the kidneys into two renal portal veins, which run forwards along the outer sides of the kidneys and supply them with blood. Blood from the alimentary canal and spleen is conveyed to the liver by a hepatic portal vein,

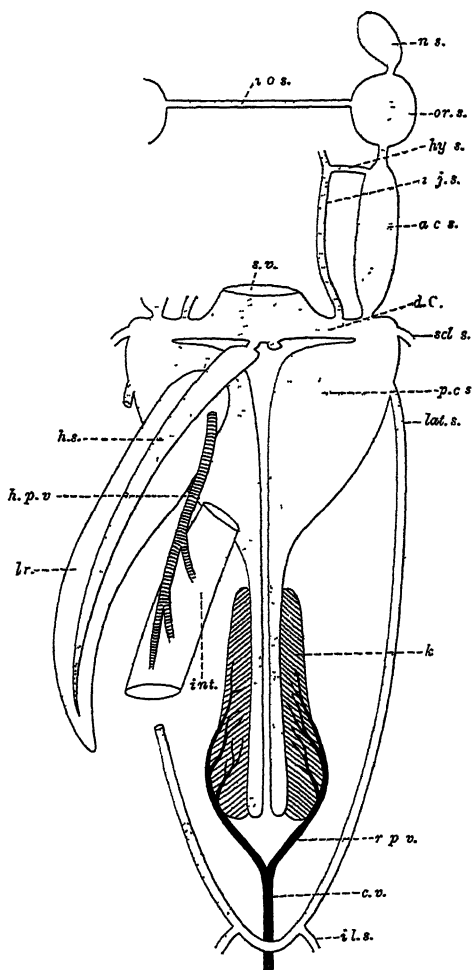


FIG. 202.—A diagram of the venous system of the dogfish.

a.c.s., Anterior cardinal sinus; *c.v.*, caudal vein; *d.C.*, ductus Cuvieri; *h.p.v.*, hepatic portal vein; *h.s.*, hepatic sinus; *hy.s.*, hyoidean sinus; *i.j.s.*, inferior jugular sinus; *i.o.s.*, interorbital sinus; *il.s.*, iliac sinus; *int.*, intestine; *k.*, kidney; *lat.s.*, lateral sinus; *lr.*, liver; *n.s.*, nasal sinus; *or.s.*, orbital sinus; *p.c.s.*, posterior cardinal sinus; *r.p.v.*, renal portal vein; *s.v.*, sinus venosus; *scl.s.*, subclavian sinus.

and thence, after passing through capillaries, is discharged into the hepatic sinuses. It will be noticed that the circulation of the dogfish contains a single circuit only, the blood from the respiratory organs being carried directly to the rest of the body without returning to the heart in the interval. Its general course is summed up in the table on p. 301.

The spinal cord of the dogfish resembles that of the frog in most respects and need not be described here. The brain, although in general features it is like that of the frog, shows considerable differences in detail. The foremost region in the middle line is the *cerebrum*, which corresponds to the cerebral hemispheres of the frog, but is single and somewhat globular in shape; its double nature is shown outwardly by a shallow longitudinal groove and internally by the presence of two lateral ventricles. The two olfactory lobes lie at the sides of the cerebrum, each arising from it by a short, stout stalk, which expands into a large mass against the olfactory capsule. The lateral ventricles of the cerebrum are continued into the olfactory lobes. The cerebrum is followed by a thalamencephalon which is somewhat longer than that of the frog. From the hinder part of its thin roof arises the long, hollow, slender pineal stalk, which runs forward over the cerebrum to end in a small swelling below the membrane which covers the anterior fontanelle. The floor of the thalamencephalon bears a hollow, backwardly directed infundibulum, which differs from that of the frog in being folded, the end passing forwards under the first part, and in bearing at the sides a pair of thick-walled *lobi inferiores* and behind these a three-lobed, thin-walled, vascular expansion known as the *saccus vasculosus*. The pituitary body is said to be a very small tube which lies below the infundibulum attached to the floor of the skull. The mid-brain, which succeeds the thalamencephalon, bears above two optic lobes which stand closer than those of the frog. The cerebellum behind them is much larger than that of the frog and oval in outline, with the long axis fore and aft, and overhangs the optic lobes in front and the thin-roofed fourth ventricle in the medulla oblongata behind it. The medulla is pro-

**Central
Nervous
System.**

duced forward into a pair of wings, the *restiform bodies*, which lie at the sides of the cerebellum.

The cranial nerves resemble in number and general distribution those of the frog, but the presence of the gills and other differences in the arrangement of the organs of the head causes the distribution to differ in detail. The olfactory nerves are a bunch of fine

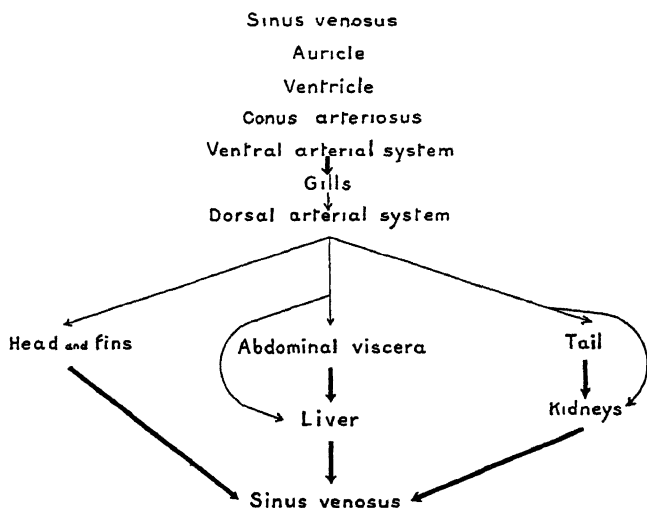


FIG. 203.—A diagram of the circulation of the blood in a dogfish. Thick lines indicate venous blood, narrow lines arterial blood.

threads which pass from the olfactory lobes of the brain into the adjoining olfactory organs. The optic nerves pass from the lower surface of the thalamencephalon, each through the optic foramen of the opposite side, to the eyeballs, crossing in a chiasma below the brain. The third or oculomotor nerve of each side, arising from the ventral surface of the mid-brain, passes outwards through its foramen into the orbit of its own side, where it supplies the superior, inferior, and internal recti muscles

of the eye by short branches and gives a long branch across the floor of the orbit to the inferior oblique. The slender fourth or patheticus nerve arises from the dorsal surface

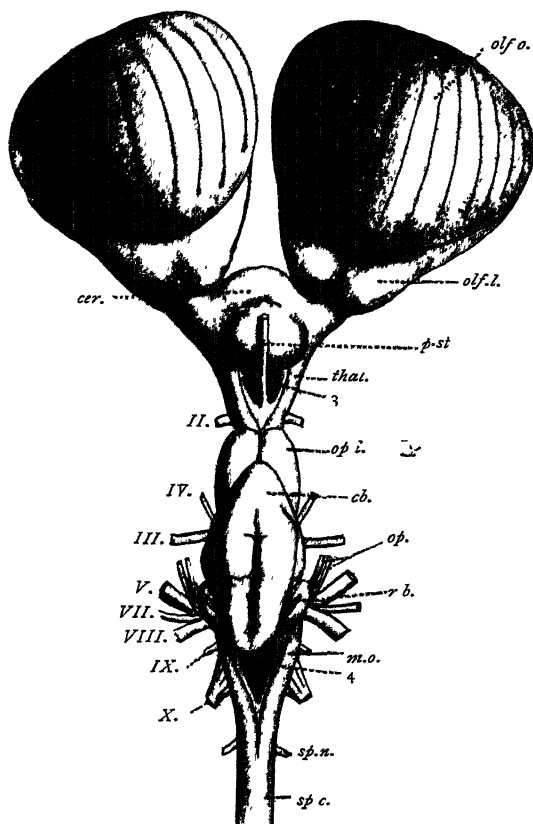


FIG. 204.—The brain of the dogfish, seen from above.

cb, Cerebellum; *cer.*, cerebrum; *m.o.*, medulla oblongata; *olf.l.*, olfactory lobe; *olf.o.*, olfactory organ; *op.*, ophthalmic branches of fifth and seventh nerves; *op.l.*, optic lobes; *p.st.*, pineal stalk; *r.b.*, restiform body; *sp.c.*, spinal cord; *sp.n.*, spinal nerve; *thal.*, thalamencephalon; 3, 4, third and fourth ventricles; *II.-IV.*, *VII.-X.*, cranial nerves

of the brain between the optic lobes and the cerebellum, and passes out through a special foramen to supply the superior oblique muscle of its side. The sixth or trochlear nerve is also slender. It arises from the ventral side of

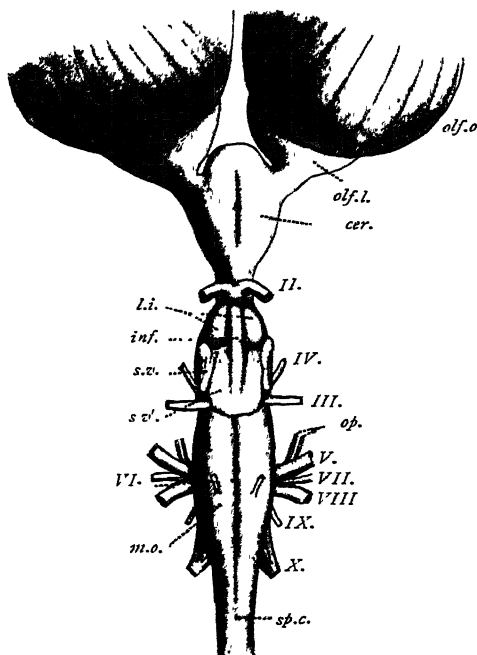


FIG. 205.—The brain of a dogfish, in ventral view.

cer., Cerebrum; *inf.*, return limb of infundibulum, sometimes regarded as the pituitary body; *l.i.*, lobi inferiores, *m.o.*, medulla oblongata; *olf.l.*, olfactory lobe; *olf.o.*, olfactory organ; *op.*, ophthalmic branches of fifth and seventh nerves; *sp.c.*, spinal cord; *s.v.*, lateral lobe of saccus vasculosus; *s.v.*, median lobe of the same; *II.-X.*, cranial nerves.

the medulla and supplies the external rectus muscle, passing through the same foramen as the main branches of the fifth and seventh nerves. The latter two nerves, with the eighth, arise close together from the sides of the medulla below the restiform body. The fifth or trigeminal has

three branches. Of these the first, or ophthalmic, parts at once from the rest of the nerve, turns forward within the skull, passes through a foramen in the side of the cranium above the recti muscles, and runs forwards along the outer side of the cranial wall, together with the similar branch of the seventh nerve, to leave the orbit by a foramen above the nasal capsule and be distributed to the skin of the snout. The rest of the nerve leaves the cranium by a large foramen below the recti muscles and runs outwards across the orbital floor as a broad band, which divides into a maxillary branch to the upper jaw and a mandibular branch to the lower. The seventh or facial nerve has an ophthalmic branch which, leaving the cranium by a foramen in front of the similar branch of the fifth, accompanies the latter, a small palatine branch which runs across the floor of the orbit behind the fifth nerve and supplies the roof of the mouth, and a large hyoidean branch which runs outwards in the hinder wall of the orbit and passes down the hyoid arch. This branch gives off a small prespiracular branch to the anterior wall of the spiracle. The palatine and hyoidean branches pass together through the same foramen with the main part of the fifth. The eighth or auditory nerve passes into the auditory capsule to supply the inner ear. The ninth or glossopharyngeal nerve arises from the side of the medulla behind and rather below the eighth, passes through a passage in the cartilage of the auditory capsule, emerges by its foramen behind the capsule, and turns down the first branchial arch, after giving off a small prebranchial branch to the hyoid arch. The tenth or vagus nerve arises by a number of roots immediately behind the ninth. It leaves the skull by a foramen beside the occipital condyle, and runs backwards along the anterior cardinal sinus, lying just median to that vessel, immediately against its lining, through which it can be seen if the vein be opened. It represents several nerves fused, and gives off across the floor of the sinus a branch to every branchial arch behind the first, each such branch bearing a prebranchial branch to the preceding arch. Shortly after leaving the skull the vagus gives off a lateral line nerve, which runs along the side of the body, rather deep

among the muscles, and supplies an organ in the skin known as the lateral line, which will be mentioned later.

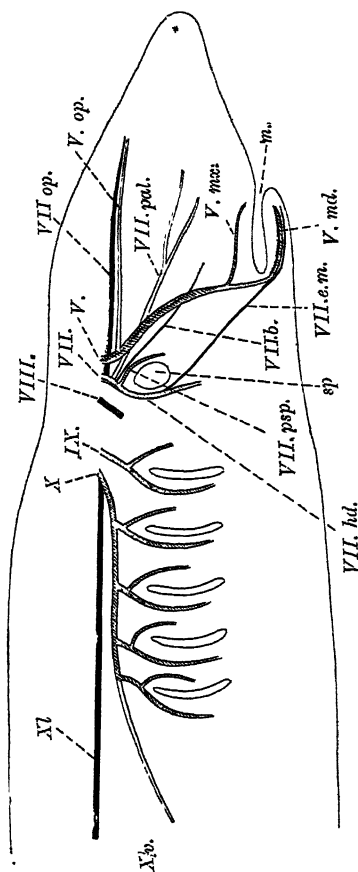


FIG. 206.—A diagram of the distribution of certain cranial nerves in the dogfish. The nerves shown in black are distributed to the system of sense-tubes which includes the neuromast ampullae, lateral line, and labyrinth of the ear. The shaded nerves are distributed to visceral arches.

V. X., Roots of the nerves; *V. md.*, *V. max.*, *V. op.*, mandibular, maxillary, and opercular branches of the fifth nerve; *VII. b.*, *VII. e.m.*, buccal and external mandibular branches of the seventh nerve, not mentioned in the text, distributed to some of the neuromast ampullae; *VII. hd.*, *VII. op.*, *VII. pal.*, *VII. psp.*, hyoid, ophthalmic, palatine, and prespiracular branches of the seventh nerve; *X. b.*, *X. e.*, lateral line and visceral branches of the tenth nerve.

After giving off the last of its branches to the branchial arches, the vagus passes downwards to supply the heart

and other viscera. The spinal nerves of the dogfish are more numerous than those of the frog, but in their general structure and arrangement resemble them. The dorsal and ventral roots by which each arises from the spinal cord pass through the wall of the neural canal by small notches in the hinder edges of the intercalary pieces and neural arches respectively. The comparison of the cranial nerves with dorsal and ventral roots of spinal nerves which was made with regard to the frog (p. 73) holds good for the dogfish and all other vertebrates. A feature of their distribution which was not obvious in the latter animal is that certain of them (the fifth, seventh, ninth, and tenth) give branches to the visceral arches. Each such branch gives off a prebranchial branch to the arch in front (in the case of the fifth nerve this branch passes to the upper jaw). The sympathetic system is irregular and difficult of dissection in the dogfish, but in the main outlines of its plan it resembles that of the frog.

Each of the olfactory organs of the dogfish is a sac enclosed in the olfactory capsule of its side of the body. It opens externally by the nostril, but has no internal opening into the mouth. Its walls are thrown into vertical folds covered with an epithelium which contains sense cells. The eyes resemble in all important respects those of the frog, and need not here be described. On account, however, of their larger size, they are more suitable objects for the study of the eye muscles. Like the eyes of the frog and those of all other vertebrate animals, each of them is moved by six muscles, which arise from the inner wall of the orbit. Four of these, known as recti, arise together near the hinder end of the orbit and diverge to be inserted into the eyeball at various points. The *rectus superior* runs outwards and forwards and is inserted into the upper side of the eyeball. The *rectus inferior* runs a similar course below the eyeball to be inserted into its lower surface. The *rectus internus* runs forwards between the eyeball and the cranial wall and is inserted into the front side of the former. The *rectus externus* runs outwards behind the eyeball, into whose hinder surface it is inserted. The remaining two muscles are known as obliqui. They arise together near the anterior end of the orbit and pass

outwards and backwards to their insertions into the eyeball. The *obliquus superior* is inserted into the dorsal surface of the eyeball just in front of the superior rectus; the *obliquus inferior* is inserted in a corresponding position in front of the insertion of the inferior rectus upon the lower side of the eyeball. By the contraction of various combinations of these muscles the eyeball may be turned in any direction.

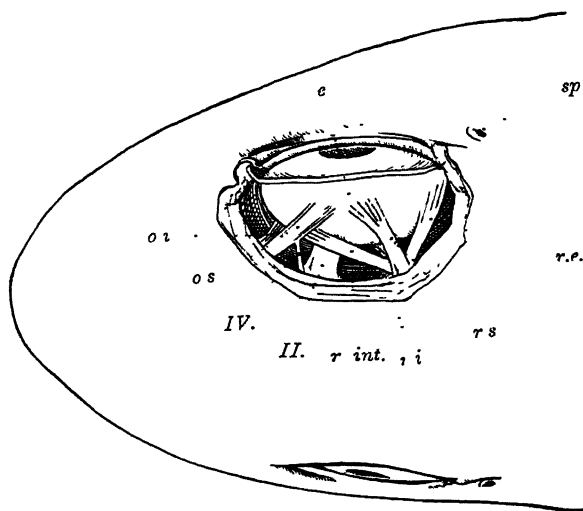


FIG. 207.—The head of a dogfish, seen from above with the right orbit opened.

e., Eyeball; *o.i.*, *o.s.*, inferior and superior oblique muscles; *r.e.*, *r.i.*, *r.int.*, *r.s.*, external, inferior, internal, and superior recti muscles; *s.p.*, spiracle; *II.*, optic nerve; *IV.*, fourth nerve.

The lower eyelid is movable. The structure of the internal ear is essentially similar to that of the frog. Its communication with the external water and the absence of a drum have already been mentioned (p. 282). Besides these sense organs, which are found in all vertebrates, fishes possess a peculiar system, known as the *neuromast organs*, which are not found in any other adult vertebrates with the exception of certain newts. These consist of sensory

supplied by a special set of nerve fibres, which join the same portion of the grey matter of the brain with which the fibres of the auditory nerve are connected, but leave the brain by various nerves, of which the principal are the ophthalmic branch of the seventh and the lateral line branch of the tenth nerve. The function of these organs is the detection of vibrations in the water of too low a frequency to be detected by the ear. The latter must be regarded as a specially highly developed part of the same system as the neuromast organs.

CHAPTER XIX

THE PIGEON¹

THE many different kinds of domestic pigeons are familiar to every one. All of them—carriers, tumblers, fantails, pouters, etc.—have been bred, by selection continued for many generations, from the wild

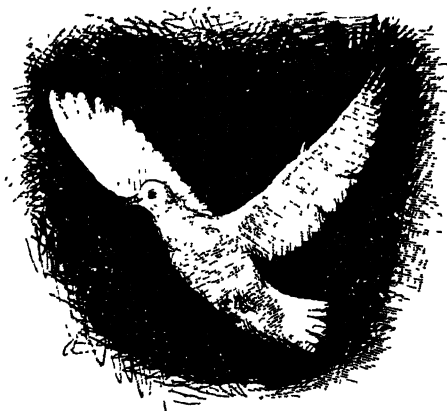


FIG. 209.—A pigeon in flight with the wings coming down.—After Marey.

Rock Dove, *Columba livia*, a bird of strong flight which is found over a great part of Europe and Asia, building among high rocks or in ruins an untidy nest of sticks, in which two white eggs are laid. It feeds on seeds of various kinds.

¹ It has been assumed, in writing this chapter, that the pigeon will usually be studied after the rabbit.

The body is boat-shaped, so as to offer little resistance to the air, and to the same end has an even contour, due to the coat of feathers, which also affords a light and warm covering. A distinct head, neck, and trunk are present, but the tail is a mere

External Features.

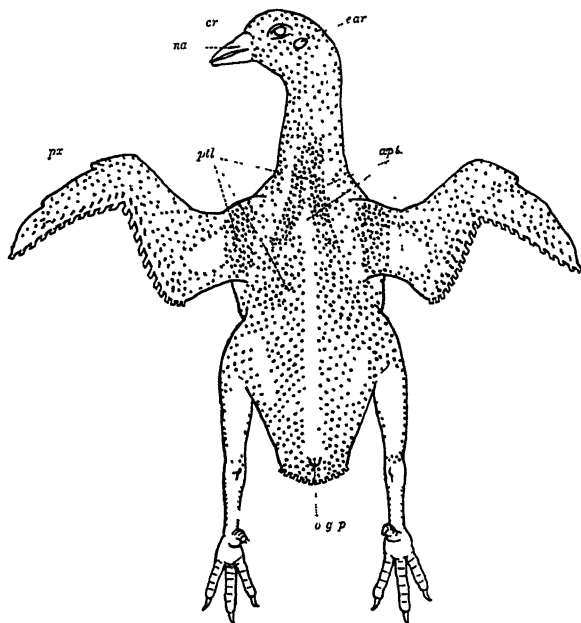


FIG. 210.—A plucked pigeon, seen in dorsal view.

apt., Apteria; *cr.*, cere, *ear*, ear; *na.*, nostril; *og.p.*, papilla on which the oil gland opens; *ptl.*, pteryx, *px.*, thumb.

stump which bears a fan of long feathers. Since the forelimbs have the form of wings, the legs must support the whole weight in standing. We shall see that the skeleton is adapted to this necessity. The feet are naked and covered with scales, which are horny and epidermic like those of a reptile, not like those of a fish. There are four toes, which have a wide tread, the first being directed backwards

and the other three forwards; the fifth is wanting. The front or facial portion of the head is drawn out into a *beak* covered with horny skin. At its base above is a swollen, featherless patch of skin, the *cere*. The nostrils lie below the cere, the eyes behind it at the sides of the head, and the

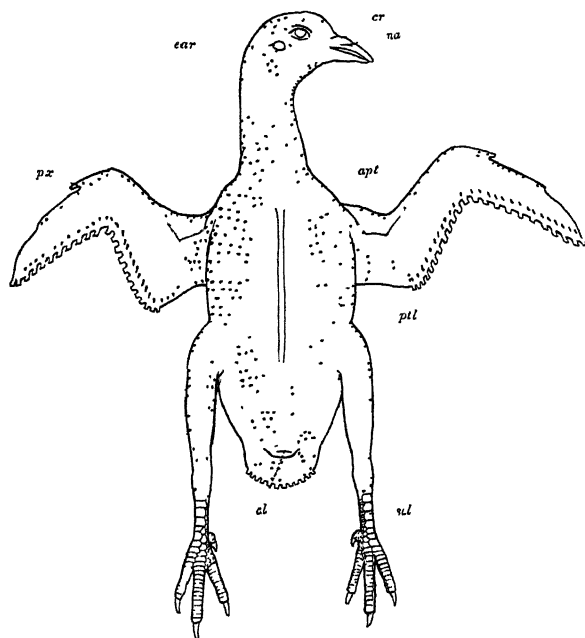


FIG. 211.—A plucked pigeon, seen in ventral view.

apt., Apterium; *cl.*, cloacal opening; *cr.*, cere; *ear*, ear; *na.*, nostril; *pil.*, pteryla; *px.*, thumb; *sc.*, scales on the foot.

ear openings below and behind the eyes, covered by feathers. There are three movable eyelids (p. 23), and the drum of the ear is at the bottom of a tube, but there is no ear flap. There is a single cloacal opening, as a transverse slit below the tail, and above the tail is a knob on which opens the *oil gland*, whose secretion is used in preening the feathers.

The feathers are epidermal structures. When the bird is plucked they are found to have been arranged in certain tracts or *pterylae*, leaving between them bare *apteria*. The feathers are of several kinds. The *quill feathers* are found along the hinder edges of the wings and tail, those on the wings being *remiges*, those on the tail

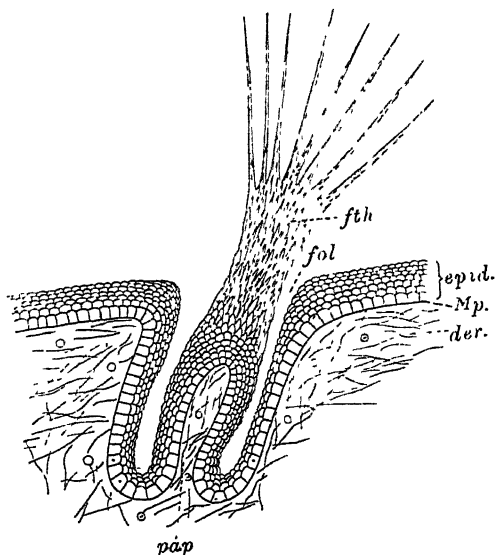


FIG. 212.—A diagram of a developing feather, highly magnified.

—From Shipley and MacBride.

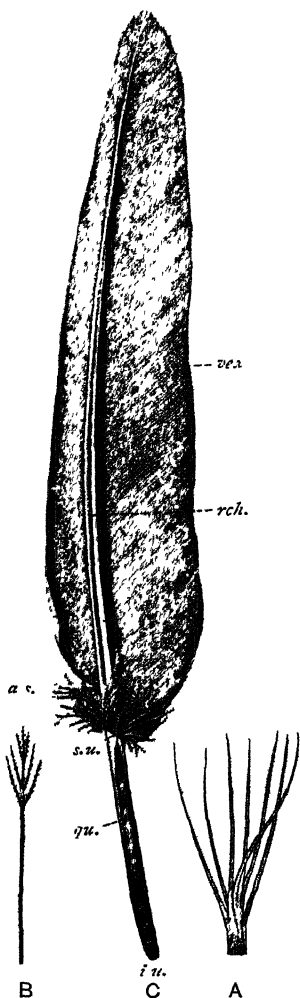
der., Dermis; *epid.*, epidermis; *fol.*, follicle; *fth*, feather; *Mp.*, Malpighian layer of epidermis; *pap.*, papilla by the growth of whose epidermis the feather is formed.

rectrices. The *contour feathers* cover the body. Those at the bases of the quill feathers are known as *coverts*. *Filoplumes* are little hair-like feathers among the contour feathers. The feathers are moulted every year and thus those damaged by use become replaced.

A quill feather consists of the following parts: The *stem or scapus* is divided into a lower, hollow part, the *calamus or quill*, and an upper,

solid part, the *rachis*. The quill is embedded in a pit of the skin and has at its lower end an opening, the *inferior umbilicus*, through which a vascular papilla projects into the growing feather. At the junction

of the quill and rachis is a minute opening known as the *superior umbilicus*. Close to this arises a small tuft known as the *aftershaft*. The rachis is the axis of the flattened part of the feather, known as the *vexillum* or *vane*. This is composed of a series of elastic plates set along the sides of the rachis with their flat sides perpendicular to the plane of the vane. The plates are known as *barbs*, and they are held together by *barbules*, which are smaller processes that fringe the barbs. The barbules of one side of a barb (distal barbules) bear little hooks or *barbicels* which catch upon the barbules of the adjoining barb. Thus the whole vane is held together and forms a single surface for striking the air. The barbules of the contour feathers are less well developed than those of the quill feathers, so that the barbs separate more easily. The filoplumes consist each of a hair-like stem with a very rudimentary vane of a few isolated barbs at its apex.



In the wing of a plucked bird there may easily be made out parts corresponding to the upper arm, forearm, and hand. In the latter the thumb is the only

Wings and Flight.

FIG. 213.—Feathers of a pigeon.

A, Down feather; B, filoplume; C, quill feather.

a s, Aftershaft; i. u., inferior umbilicus; qu., quill or calamus; rch., rachis or shaft; s. u., superior umbilicus; vex, vexillum or vane.

digit that projects. A fold of skin known as the *propatagium* connects the shoulder with the forearm in front, and a small *postpatagium* of the same kind lies across the armpit. The greater part of the surface of the wing, however, is provided by the row of twenty-three remiges along the hinder side of the limb. The remiges borne upon the hand are eleven in number and are known as *primaries*. These on the forearm are known as

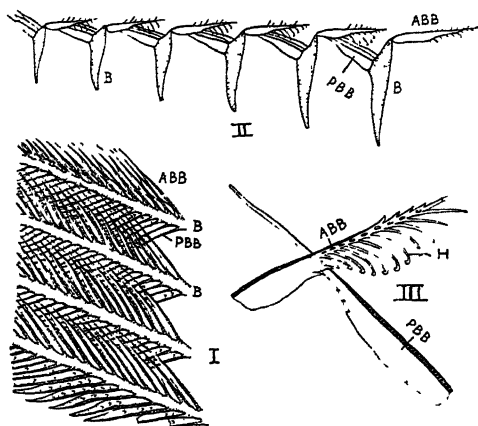


FIG. 214.—Parts of a feather.—After Nitzsch.

I., Four barbs (*B.*) bearing anterior barbules (*A.B.B.*) and posterior barbules (*P.B.B.*); *II.*, six barbs (*B.*) in section, showing interlocking of barbules; *III.*, anterior barbule with barbicels (*H.*).

secondaries. A tuft of feathers on the thumb is the *bastard wing*. In flight the wing strikes downwards and backwards in an oblique direction so as to keep the bird raised in the air and drive it forwards. In rising the angle is altered and the wing strikes more downwards. In gliding to the ground the wings are outspread and serve to check the fall. The tail feathers can be spread out on one or both sides, and are used for steering and to check the "way" of the bird, as in alighting. The downstroke of the wing is more powerful

than the upstroke, which is helped by the fall of the body when the upstroke ceases to raise it.

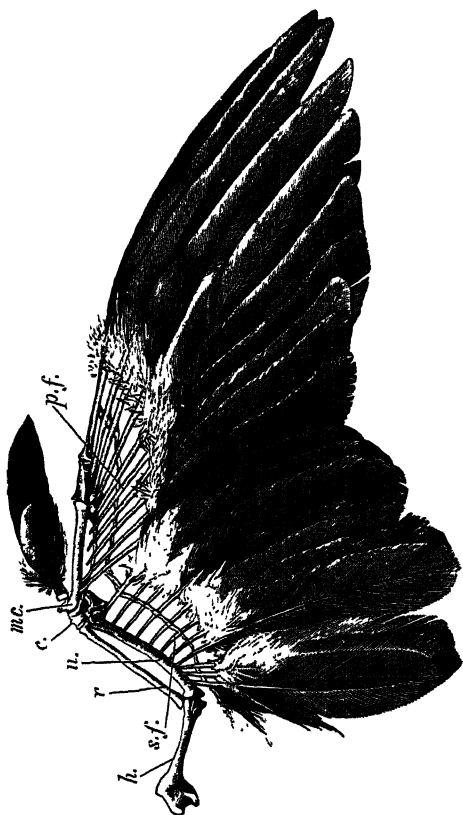


FIG. 215.—The wing of a dove.—From Thomson.
c., Carpals; *h.*, humerus; *m.c.*, carpo-metacarpus; *p.f.*, primary feathers,
r., radius; *s.f.*, secondary feathers; *u.*, ulna.

**Internal
Organs :
Skeleton.**

The pigeon is a backboned animal, and its structure is on the same general plan as that of the frog and dogfish. It has a chest or thorax, walled by ribs and a broad breastbone, but lacks the midriff or diaphragm of mammals. It is of the pentadactyle type and its skeleton resembles in main outlines that of the

frog. The bones are very light and spongy in texture and most of them, except those of the tail, forearm, hand, and hind

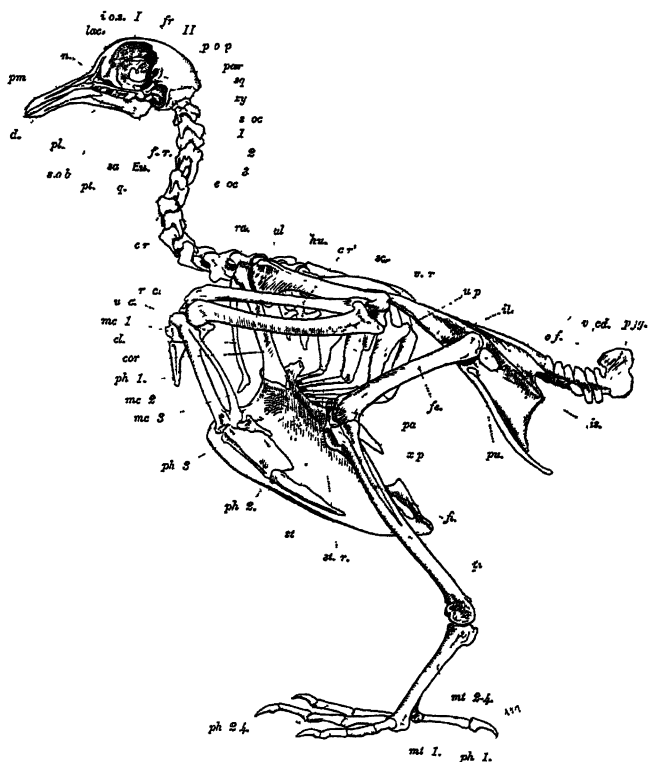


FIG. 216.—The skeleton of a pigeon, seen from the left side.

c.r., Fixed cervical rib; *c.r'*, free cervical ribs; *cl.*, clavicle; *cor.*, coracoid; *d.*, dentary; *Eu.*, Eustachian tube; *e.oc.*, exoccipital; *f.r.*, fenestral recess; *fe.*, femur; *fi.*, fibula; *fr.*, frontal; *hu.*, humerus; *i.o.s.*, interorbital septum; *il.*, ilium; *is.*, ischium; *lac.*, lacrymal; *mc. 1-3*, metacarpals; *mt. 1-4*, metatarsals; *n.*, nasal; *o.f.*, obturator foramen; *pa.*, patella; *par.*, parietal; *ph. 1-4*, phalanges; *pl.*, palatine; *pm.*, premaxilla; *p.o.p.*, postorbital process of frontal; *pt.*, pterygoid; *pu.*, pubis; *pyg.*, pygostyle; *q.*, quadrate; *r.c.*, radial carpal; *ra.*, radius; *s.o.b.*, suborbital bar; *s.oc.*, supraoccipital; *sa.*, supra-angular; *sc.*, scapula; *sq.*, squamosal; *st.*, sternum; *st.r.*, sternal ribs; *ti.*, tibia; *u.c.*, ulnar carpal; *u.p.*, uncinat process; *ul.*, ulna; *v.cd.*, caudal vertebrae; *v.r.*, vertebral rib; *x.p.*, xiphoid process; *zy.*, zygomatic process of the squamosal; *I.*, *II.*, foramina for first two cranial nerves; *1-3*, first three cervical vertebrae.

limb, contain air spaces. A tendency to the fusion of bones is seen in various regions, and the proportion of cartilage is very small. The backbone is divided into five regions: (1) The neck contains thirteen to fifteen cervical vertebræ, the commonest number being fourteen. The ends of the centra of these are of a peculiar shape known as *heterocœlous*. In front they are saddle-shaped, concave from side to side, and convex from above downwards: behind they have these curvatures reversed. The third to the eleventh or twelfth cervical vertebræ bear short ribs fused to the centra and transverse processes. The ribs of the last two are free, but do not reach the breastbone. (2) Behind these come five thoracic vertebræ, whose ribs reach the breastbone. Of

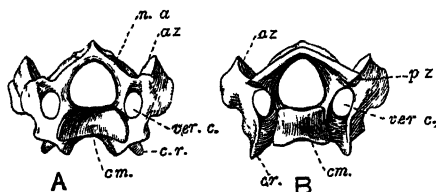


FIG. 217.—Cervical vertebræ of a pigeon.

A, From in front; B, from behind.

a.z., Prezygapophysis; c.r., cervical rib; cm., centrum; n.a., neural arch; p.z., postzygapophysis; ver.c., foramen of transverse process.

these the first three are fused together, the fourth is free, and the fifth is fused with those behind it. (3) The next half-dozen vertebræ are known as lumbar and are fused in front with the last thoracic and behind with (4) the two sacral and (5) the first five caudals. Thus there is a long group of fused vertebræ, known as the sacrum, to which the pelvic girdle is attached. Then follow six free caudals and the *ploughshare bone* or *pygostyle*, which consists of four fused vertebræ and supports the tail. Each rib has a head or capitulum which articulates with the centrum of its vertebra and a tubercle which articulates with the transverse process. Those which join the sternum are bent forwards at an angle to do so, the part above the angle being known as the vertebral rib, that below as the sternal rib. Both

parts are bony in the pigeon, whereas in the rabbit the sternal ribs are cartilaginous. On the hinder side of each of the free ribs, except those of the last pair, is an *uncinate process*. The skull is remarkable for the fusion of most of its bones. There is a short, wide cranium, lying mainly behind the large orbits, which are separated, not by the cranium, but by an *interorbital septum*. A scaffolding of slender jawbones supports the beak.

The hinder part of the cranium is formed by two exoccipitals at the sides of the foramen magnum, a median basioccipital below and a

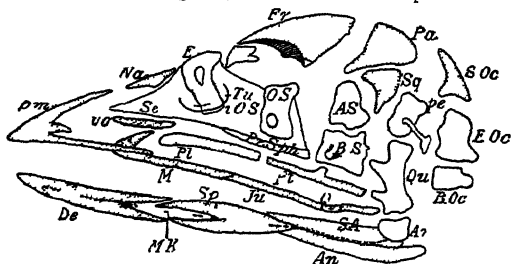


FIG 218 — A diagram of a bird's skull, disarticulated —
After Gadow. Membrane bones shaded

B Oc, basioccipital *E Oc*, exoccipital *S Oc*, supraoccipital
Pa, parietal *Fr*, frontal *Na*, nasal *pm*, premaxilla,
M, maxilla *Ju*, jugal *Qu*, quadratojugal *Qu*, quadrate
Pl, palatine *Pt*, pterygoid *pe*, petrotic *Sq*, squamosal
AS, alisphenoid, *BS*, basisphenoid, *OS*, orbito
sphenoid *Pr Sph*, presphenoid *vo*, vomer *ioS*, inter
orbital septum *E*, ethmoid *Se*, nasal septum *De*
dentary *Sp*, splenial *An*, angular *SA*, supra angular
Ar, articular *MK*, Meckel's cartilage

median supraoccipital above. There is one median occipital condyle, formed mainly by the basioccipital. The roof of the cranium in the middle and foremost regions is formed by the parietals and frontals. In the region of the parietals the floor is formed by the basisphenoid, which lies in front of the basioccipital, but is covered in below by a broad membrane bone, the basitemporal, which perhaps corresponds to the crosspiece of the parasphenoid. The side of the skull in this region is formed mainly by the squamosal, from which a zygomatic process projects forwards, lying free. Below the squamosal the wall is derived in front from the alisphenoid and behind from the bones of the auditory capsule united with adjoining bones, but the limits of none of these can be made out. In the frontal region the cranial cavity is greatly restricted by the presence of the interorbital septum, over which, however, it extends forward somewhat. The septum is

formed by the union of mesethmoid with presphenoid and orbitosphenoid elements to form a single plate of bone with a thickened ventral edge, known as the rostrum, representing the blade of the parasphenoid. The frontal sends downward a postorbital process. The lacrymal of each side is a small, flat curved bone in front of and above the orbit. In the olfactory region the nasals are a pair of thin bones in the roof, before the frontals. Their fore edges are deeply notched for the nostrils. The vomers of the pigeon are vestigial. In the common fowl they are represented by a slender median rod in front of the rostrum. In the upper jaw the palatines are a pair of slender

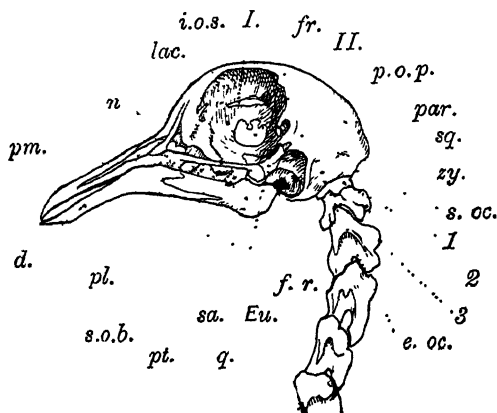


FIG. 219.—The skull and some of the cervical vertebrae of a pigeon, from the left side.

d., Dentary; *Eu.*, Eustachian tube; *e.oc.*, exoccipital; *f.r.*, fenestral recess; *fr.*, frontal; *i.o.s.*, interorbital septum; *lac.*, lacrymal; *n.*, nasal; *par.*, parietal; *pl.*, palatine, *pm.*, premaxilla; *p.o.p.*, postorbital process of frontal; *pt.*, pterygoid; *q.*, quadrate; *s.o.b.*, suborbital bar; *s.oc.*, supraoccipital; *sa.*, supra-angular; *sq.*, squamosal; *zy.*, zygomatic process of the squamosal; *I.*, *II.*, foramina for first two cranial nerves; 1-3, first three cervical vertebrae.

bars placed lengthwise in the roof of the mouth. From the hinder end of each a short, stout pterygoid slopes outwards and backwards to join the quadrate, which is a strong, three-branched bone articulated above with the squamosal, in front with the pterygoid, and below with the lower jaw, whose suspensorium it forms. The premaxilla of each side is a large, triradiate bone with the main part directed forward and fused with its fellow to form the tip of the beak, while two other processes pass back to join the two forward processes of the nasal and thus enclose the nostril. The maxilla is a rod lying inside the lower backward process of the premaxilla and projecting backward beyond it. It gives off a plate of bone, the maxillopalatine

process, on its inner side. A slender splint, the jugal, joins it to a third slip, the quadrato-jugal, which articulates with the outside of the lower end of the quadrate. Thus there is formed a fine suborbital bar. In the slender lower jaw, articular, angular, supra angular, dentary, and splenial elements can be made out. There is a columella auris and a slender, mainly bony, forked hvoid apparatus.

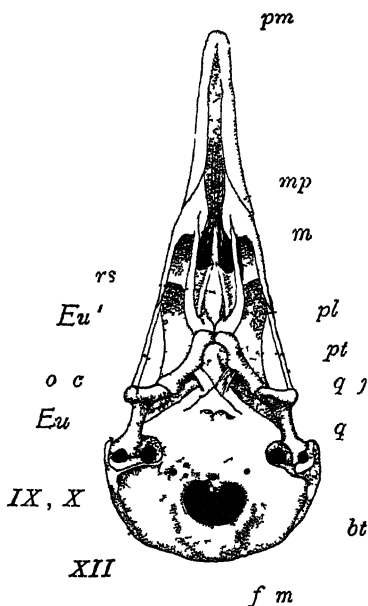


FIG 220—The skull of a pigeon, seen from below

bt, Basitemporal *Eu* hinder opening of passage for Eustachian tube *Eu* anterior opening of the same, *f m*, foramen magnum *m*, maxilla *mp* maxillopalatine process *oc* occipital condyle *pl*, palatine *pm* premaxilla *pt*, pterygoid *q*, quadrate *qj*, quadrato-jugal *rs* rostrum *IX, X*, *XII*, foramina for cranial nerves

The shoulder girdle contains narrow, sabre-like scapulæ, stout coracoids which slope down to join the sternum, and slender clavicles which join to form the "merry thought". Where scapula, coracoid, and clavicle join a small opening, the *foramen triosseum*, is left between them. The sternum is a broad plate, bearing below a conspicuous median keel for the attachment of the great wing muscles, behind two xiphoid processes, at the sides facets for the ribs, and in front surfaces for the articulation of the coracoid bones. In the wing skeleton there is a short, stout humerus,

a parallel radius and ulna, rather widely separated except at their ends, where they touch, only two free carpal bones, those of the second row having fused with the metacarpals, of which there are three, fused together, and three digits. The thumb has one joint, the first finger two, and the

second one. In the pelvic girdle there is a long ilium connected with the sacrum along nearly the whole of its inner side. This, together with the length of the sacrum, enables the trunk to be supported by the single pair of legs in a more or less horizontal position. The acetabulum is placed near

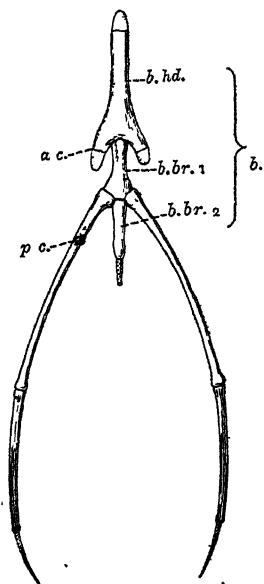


FIG. 221.—The hyoid apparatus of a pigeon.

a.c., Anterior cornu; *b.*, body of the hyoid; *b.br.1*, *b.br.2*, basibranchials; *b.hd.*, basihyoid; *p.c.*, posterior cornu.

the middle of the ilium. The ischium is a flat, backwardly directed bone, and the pubis is slender and also directed backwards. In many birds it has a small *prepubic process* in front. There is no symphysis or ventral junction of the girdles. The hind-limb has a short, stout femur, a long tibia, a slender fibula, partly joined to the tibia below, no free tarsals, these bones being fused to the tibia and metatarsals, a single tarso-metatarsus formed by the union of the distal tarsals with the metatarsals (except the small, free, first metatarsal), and four toes, each of several joints.

The most conspicuous part of the muscular system is the great *pectoralis major*, arising from the sternum and clavicle, is inserted on the under side of the humerus, which it pulls downwards, thus raising the bird and driving it forward by the wing-beat in flight.

Muscular Arrangements.

The smaller *pectoralis minor* arises from the sternum above the major and passes through the foramen triosseum and over the shoulder to its insertion on the upper side of the humerus, which it raises. The perching mechanism is also interesting. The flexor tendons which curve the toes round a branch are so arranged that they are tightened by the bending of the metatarsus on the tibia

in perching, so that the bird does not fall even when it is asleep.

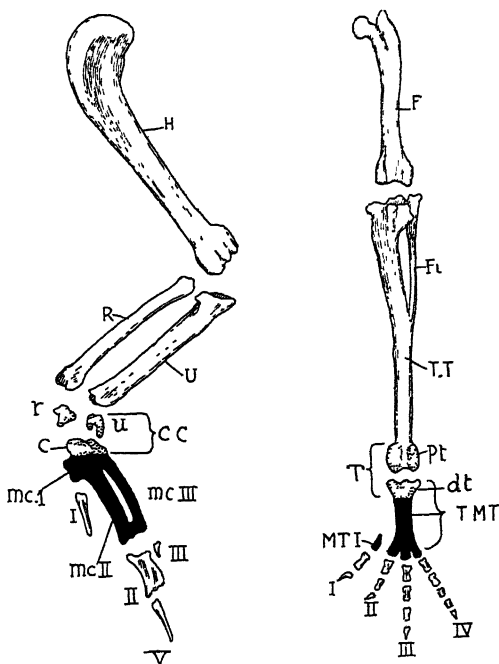


FIG. 222.—The fore-limb and hind-limb of a bird compared.
—From Thomson.

H., Humerus; *R.*, radius; *U.*, ulna; *r.*, radiale; *u.*, ulnare; *C.*, distal carpal region united to carpo-metacarpus; *CC.*, the whole carpal region; *MC.I.*, metacarpal of the thumb; *I.*, phalanx of the thumb; *MC.II.*, second metacarpus; *II*, second digit; *MC.III.*, third metacarpus; *III.*, third digit. *F.*, femur; *T.T.*, tibio-tarsus; *Fi.*, fibula; *Pt.*, proximal tarsals united to lower end of tibia; *dt.*, distal tarsals united to upper end of metatarsus, forming a tarso-metatarsus (*T.MT.*); *T.*, entire tarsal region; *MT.I*, first metatarsal, free; *I.-IV.*, toes.

The mouth has no teeth, no true palate or false roof like that of the rabbit, large posterior nares partly hidden by soft palatal folds, a single opening for the Eustachian tubes, and a sharp-pointed tongue. The glottis is not protected by an epiglottis as

Alimentary System.

in the rabbit. The gullet widens into a thin-walled *crop*, in which the food is stored. From the crop the canal continues to the *fore-stomach* or proventriculus, a glandular part of the stomach, where the gastric juice is secreted. This is followed by the *gizzard*, a lens-shaped chamber with very thick muscular walls and a horny lining, where the food is ground up by the aid of small stones which have been swallowed. It lies below the proventriculus, which opens

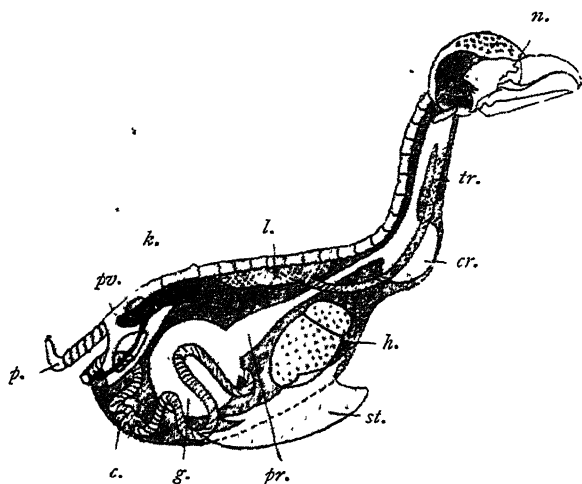


FIG. 223.—The position of organs in a bird.—After Selenka.

n., Nostrils; *tr.*, trachea; *cr.*, crop; *h.*, heart; *st.*, sternum; *pr.*, proventriculus; *g.*, gizzard; *c.*, caeca; *p.*, pygostyle; *pv.*, pelvic girdle; *k.*, kidney; *l.*, lung.

on its dorsal border, rather to the left side: on the right side near the same spot is the opening of the duodenum. This is a V-shaped loop, between whose limbs lies the pancreas. The ducts of this gland are three, and all open into the distal limb of the duodenum, two about the middle of its length and one, which is longer than the others, near the end. There are two bile ducts, which run from the large, bilobed liver and join the duodenum, the wide left duct opening into the proximal limb and the

narrower right duct into the distal limb near the first two pancreatic ducts. There is no gall bladder in the common pigeon. The ileum is a much coiled tube about two and a half feet in length. The rectum is about an inch and a half long. Its beginning is marked by a pair of small *rectal cæca*, behind it passes into the cloaca. This has three regions separated by shelves of the wall. The first and largest is the *coprodæum* into which the rectum opens, the small middle division is the *urodæum* into which the urinary and generative ducts open, the third, of medium size, is the *proctodæum*, upon its dorsal surface there opens in the young a glandular sac, the *bursa Fabricii*, of unknown function.

The glottis, behind the root of the tongue, opens into the voiceless larynx, from which the long trachea, strengthened with bony rings, leads back along the neck, lying at first below the gullet and then at its left side. At the base of the neck it divides into the two bronchi, these run outwards and backwards to the lungs, which lie against the dorsal walls of the thorax covered with peritoneum below only. The hinder end of the trachea is dilated and forms, with the beginnings of the bronchi, the *syrinx* or organ of voice. Sound is produced by the vibration of the *membrana semilunaris*, a delicate vertical fold of mucous membrane extending forwards from the angle between the bronchi. The latter not only give off tubes which branch and form the spongy lungs, but also pass right through these organs and are connected with a system of large *air sacs*, of which there are altogether nine, named, from behind forwards, the abdominals, posterior thoracics, anterior thoracics, cervicals, and inter-clavicular. Certain of the air sacs are connected with air spaces in the bones. This arrangement adds somewhat to the lightness of the bird, but is probably of greater

Respiratory Organs

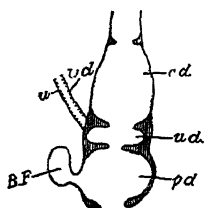


FIG 224 — A diagrammatic section of the cloaca of a male bird — After Gadow

cd Upper region of cloaca into which rectum opens *ud*, median region into which ureter (*u*) and vas deferens (*vd*) open from each side *pd* posterior region into which bursa Fabricii (*BF*) opens

of the *membrana semilunaris*, a delicate vertical fold of mucous membrane extending forwards from the angle between the bronchi. The latter not only give off tubes which branch and form the spongy lungs, but also pass right through these organs and are connected with a system of large *air sacs*, of which there are altogether nine, named, from behind forwards, the abdominals, posterior thoracics, anterior thoracics, cervicals, and inter-clavicular. Certain of the air sacs are connected with air spaces in the bones. This arrangement adds somewhat to the lightness of the bird, but is probably of greater

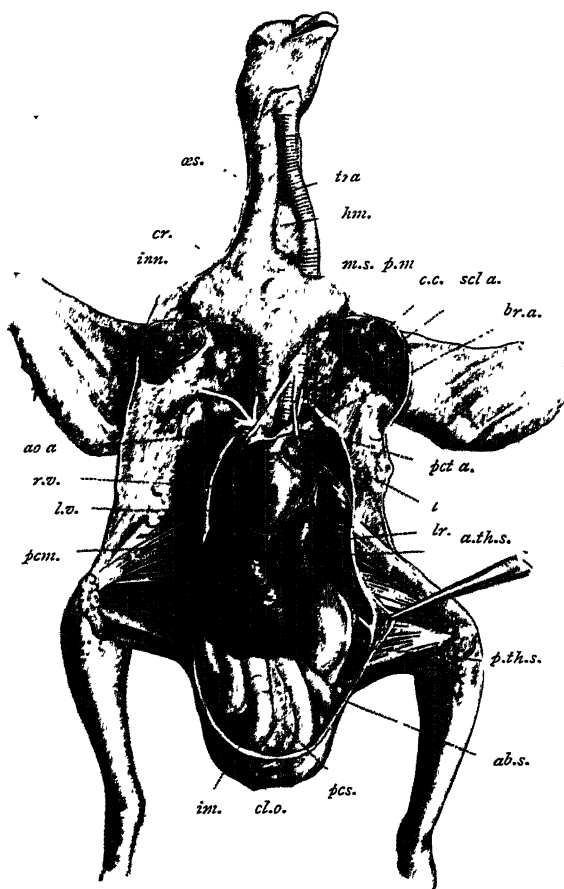


FIG. 225.—A pigeon opened from the ventral side to show the principal organs in their natural positions.

a.th.s., Anterior thoracic air sac, *ab.s.*, abdominal air sac; *ao.a.*, aortic arch; *br.a.*, brachial artery; *c.c.*, common carotid artery; *cl.o.*, cloacal opening; *cr.*, crop; *im.*, ileum; *inn.*, innominate arteries; *l.*, lung; *l.v.*, left ventricle; *lr.*, liver; *m.s.*, muscles concerned in the movements of the syrinx; *æs.*, oesophagus; *p.m.*, pectoralis major muscle; *p.th.s.*, posterior thoracic air sac; *p.cm.*, pericardium (torn open); *p.c.s.*, pancreas; *p.c.a.*, pectoral artery; *r.v.*, right ventricle; *scl.a.*, subclavian artery; *thm.*, thymus; *tra.*, trachea. The gizzard is seen opposite the forceps which hold back the abdominal wall.

importance in raising the efficiency of its respiration by increasing the flow of the air through the bronchi. Respiration is brought about mainly by expiration, not by pumping in air, as in the frog, or active inspiration, as in the rabbit.

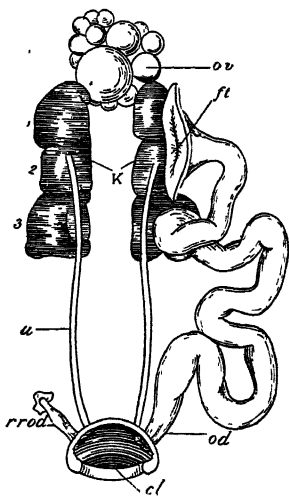


FIG. 226.—The urogenital organs of a female pigeon. —From Thomson.

K., Kidney (metanephros) with three lobes; *u.*, ureter; *cl.*, cloaca; *ov.*, ovary; *od.*, oviduct; *f.t.*, funnel at end of oviduct; *r.od.*, rudimentary right oviduct.

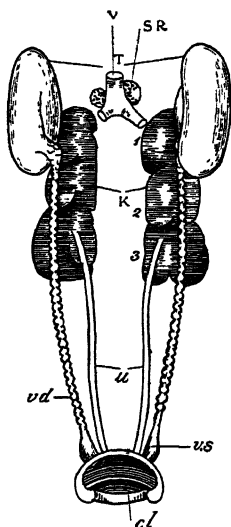


FIG. 227.—The urogenital organs of a male pigeon. —From Thomson.

T., Testes; *V.*, base of inferior vena cava; *S.R.*, suprarenal glands; *K.*, kidneys with three lobes (1, 2, 3); *u.*, ureter; *v.d.*, vas deferens; *v.s.*, seminal vesicle; *cl.*, cloaca.

The movements of breathing consist in the rise and fall of the sternum, which compresses the air sacs and lungs.

The kidneys are metanephric (p. 290). They lie in the back under the sacrum as a pair of three-lobed bodies. From the hinder lobe of each a ureter runs back to the cloaca. There is no bladder. The sexes are, of course, separate. The testes lie in front of the kidney. From each of them the vas

Excretory and Reproductive Organs.

deferens, corresponding to the Wolffian duct of the dogfish and frog, runs back on the outer side of the ureter to end in a small swelling or seminal vesicle which opens into the cloaca. When it is full of ripe sperm the vas deferens is slightly convoluted. There being no penis, the sperm is passed in coition by the cloaca of the male being closely apposed to that of the female. The adult pigeon has only one ovary, that of the right side having atrophied early in life. The right oviduct also atrophies, but a small vestige remains, attached to the cloaca. The ovary is covered with follicles which contain ova in various stages of ripeness. The oviduct is a wide, twisted tube, thin-walled in front and thick behind, opening into the body cavity by a long funnel just behind the ovary. When the ova are ripe they are shed into the body cavity and immediately caught by the opening of the oviduct. Each ovum is a large, round, yellow body corresponding to the "yolk" of the egg. It is a single gigantic cell, so full of yolk that the protoplasm is practically restricted to a small patch at one side, containing the nucleus. It is fertilised in the thin region of the oviduct, coated with white of egg in the first part of the thick region, and provided with a double membrane and a porous chalky shell in the hinder part. The eggs are hatched by the warmth of the body of the parents, who sit upon them in turns. The young, which emerge after sixteen days, are provided with a scanty yellow *down* and, unlike young chickens, are at first quite helpless, with closed eyelids. They are fed by their parents with a creamy fluid known as "pigeon's milk" formed by the breaking down of the epithelium of the crop. They are fledged at the end of three weeks, and after a few days' education in flight by their parents go out into the world for themselves.

The blood has a temperature of 42° C., which is higher than that of mammals. This fact is no doubt connected with the active life of the bird and the rapid metabolism which it necessitates. We have already seen how the respiratory organs provide the ample supply of oxygen which such metabolism demands. The red corpuscles are oval and nucleated. The heart has four chambers, two auricles and two ventricles, there being no

sinus venosus or conus arteriosus. The impure blood returned by the venæ cavæ to the right auricle passes into the right ventricle through an opening guarded by a muscular valve without chordæ tendineæ. It is then driven by the pulmonary artery to the lungs, whence it returns by the pulmonary veins to the left auricle, passing thence through two membranous valves with chordæ tendineæ to the left ventricle, by which it is driven into the single aortic arch. The openings of the aorta and pulmonary artery are guarded each by three semilunar valves. The aortic arch bends over to the *right* side, giving off at its apex right and left innominate arteries, from each of which arise a carotid and a subclavian. The latter is exceedingly short, breaking up immediately into brachial and pectoral branches. The further course of the arteries is shown in the diagram (Fig. 288). The venous system is shown in the same figure. There are three venæ cavæ, as in the frog. Each superior vena cava is formed by the union of a jugular, a brachial, and a pectoral. The jugulars anastomose under the base of the skull. The inferior vena cava arises by the junction of two iliac veins in front of the kidney. Each iliac vein is formed by the union of a femoral, a renal, and a big hypogastric which passes upwards through the kidney. Behind the kidneys the hypogastrics arise in the following

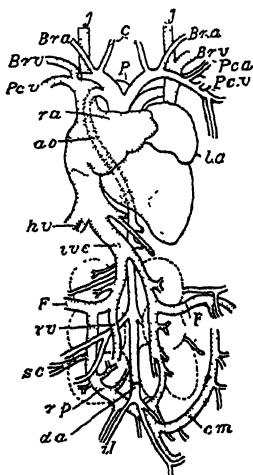


FIG. 228.—A diagram of the principal arteries and veins of a pigeon.—From Thomson, after Parker.

ao., Aortic arch; Br.a., brachial artery, Br.v., brachial vein; C., carotid artery, c.m., coccygeo-mesenteric vein; d.a., dorsal aorta; F., femoral vein adjoining femoral artery; h.v., hepatic veins; i.l., internal iliac artery and vein; i.v.c., inferior vena cava; j., jugular vein; l.a., left auricle; P., right pulmonary artery; P.c.a., pectoral artery; P.c.v., pectoral vein, r.a., right auricle; r.p., hypogastric vein; r.v., renal vein; s.c., sciatic artery and vein. Near the apex of the ventricle the coeliac and anterior mesenteric arteries and the epigastric vein are shown, but not lettered. At the hinder end of the figure the caudal and posterior mesenteric vessels are shown, but not lettered.

way: The little caudal vein forks into two branches, each of which runs through one of the kidneys as a hypogastric. Each hypogastric is much larger than the caudal of which it is a branch, because at the bifurcation another vein, the coccygeo-mesenteric from the cloaca and large intestine, joins the caudal, and immediately after it has separated from its fellow the hypogastric

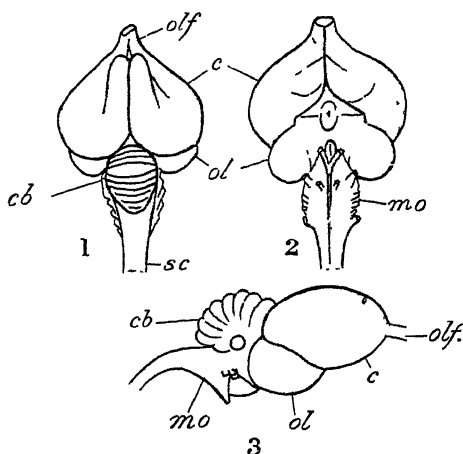


FIG. 229 —The brain of a pigeon.—From Thomson.

- (1) Dorsal, (2) ventral, and (3) side view. *c.*, Cerebral hemispheres; *cb.*, cerebellum; *m.o.*, medulla oblongata; *o.l.*, optic lobes; *olf.*, olfactory lobes; *s.c.*, spinal cord.

receives an internal iliac vein. In its course through the kidney it receives several small renal veins and a sciatic. There is practically no renal portal system, though the femorals give a few small branches to the kidneys. A hepatic portal system exists as usual. A vein known as the epigastric takes blood from the great omentum, or sheet of fat which covers the abdominal viscera, to the left hepatic vein. It represents the anterior abdominal vein of the frog.

The cerebral hemispheres of the brain are large, smooth, and rounded. The roof of the lateral ventricles is thin. The olfactory lobes are very small. **Nervous System and Sense Organs.** The cerebellum and cerebrum meet over the thalamencephalon, thrusting the optic lobes to the sides, where they project as two round, hollow masses. The cerebellum is ridged transversely. There are twelve cranial nerves, corresponding to those of the rabbit (p. 364). The sense of smell is not well developed. Hearing is acute, the labyrinth possessing the organ known as the cochlea which was quite rudimentary in the frog. Sight is very keen, and the eye is remarkable for the presence of a vascular pigmented organ, known as the *pecten*, which protrudes into the vitreous humour from the "blind spot" where the optic nerve enters.

CHAPTER XX

THE RABBIT

THE Rabbit, *Lepus cuniculus*, is one of the animals that have been introduced into Britain by man.

Habits. Its original home was in the countries at the western end of the Mediterranean. Thence it has spread or been carried by man throughout most of Europe and into various other parts of the world, where its adaptability and great fertility have enabled it to thrive to such an extent that often, as notably in Australia, it has become a serious nuisance. Its habits are well known. It is herbivorous, and will eat a great variety of plants. It is gregarious, and digs for itself burrows into which it retires to sleep or at the approach of danger and to rear its young. On this account it prefers districts where the soil is light and easily worked, though it will live even in wet places if these bear dense vegetation, in which it can form runs instead of burrows. As befits its defencelessness, it is very wary, and its habit of living in societies gives each individual a better chance of receiving warning of the approach of an enemy. Perhaps its custom of feeding chiefly at dusk is a similar precaution. It lives seven or eight years and breeds four times, or oftener, in a year, beginning to breed at six months old. As each litter contains from five to eight young, its natural rate of reproduction is enormous and enables it to pay the heavy toll taken by its numerous enemies. It is readily domesticated, and various fancy races have been produced by breeders.

The rabbit is covered with *fur*, which in the wild race is of an inconspicuous, tawny-grey colour save on the under side of the short upright tail, where it is white. When, on an alarm, the animal scampers off to its burrow, the white patch on its

**External
Features.**

tail is conspicuous, and this, though no doubt it enables an enemy to follow the fugitive, has probably advantages to the species in guiding and warning other members of the society. The head is separated from the trunk by a distinct *neck*, a feature which we have not met with in the dogfish or frog. The long *external ears or pinnae* are another new feature. The eyes have *movable upper and lower lids* with a few *eyelashes*, and a small third eyelid lies as a white membrane in the inner corner and is used in cleaning the cornea. This eyelid is rudimentary in man. The nostrils are two oblique slits at the end of the snout, and lead internally into the pharynx. We have seen that in the dogfish the nostrils do not open internally and in the frog they open into the front of the mouth. The upper lip is a "hare lip," cleft in the middle, the cleft being continuous with the nostrils and exposing the great front teeth. On the sides of the snout and round the eyes there are strong tactile hairs or *vibrissae* which correspond to the so-called "whiskers" of the cat. There is *no cloaca*, the anus and urinogenital openings being separate, and the latter in front of the former, in the male on the end of a *penis*, in the female within a slit-like *vulva* which contains in front a small *clitoris* corresponding to the penis. Beside the penis in the male lie the *scrotal sacs*, into which the testes of the adult descend, but there is no hanging scrotum. Along the breast and belly of the female there are four or five pairs of *teats or mammae*, on which open the milk glands which we meet here for the first time. At the sides of the anus are a pair of hairless depressions, into which open the ducts of the *perineal glands*, to whose secretion is due the peculiar smell of the rabbit. The limbs have the same general shape as those of the frog and other land vertebrates, being of the type known as *pentadactyle*, though in the rabbit, while the fore-limbs have five digits, the hind-limbs have only four. The digits end in horny *claws*. The fore-limbs are shorter than the hind-limbs, and in running the animal does not tread upon the whole sole of the foot, carrying the heel above the ground.

The closely related Common Hare differs from the rabbit in its smaller size, the greater length of the hind-limb, the black tips of the very long ears, the absence of

the burrowing habit, and the fact that the young, which are born in the open, are hairy, whereas those of the Hares. rabbit, born in the shelter of a burrow, are naked. The hare is a native of Britain and other parts of Northern Europe. The Mountain Hare is more like the rabbit in the shape of its body, but has black tips to the ears and turns grey or white in cold weather.

The rabbit is a backboned animal, with all that we have seen that to imply. Like that of all Vertebrata, its skin is

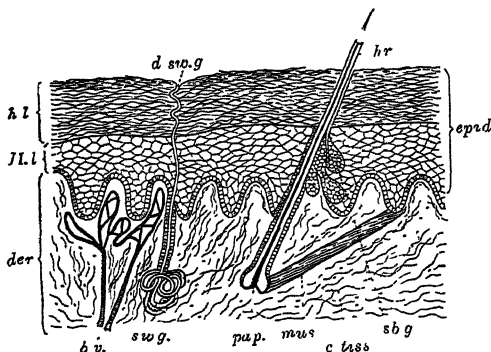


FIG. 230.—A diagram of a section through the skin of a mammal. Highly magnified.—From Shipley and MacBride.

b.v., Blood vessels; *c.tiss.*, connective tissue of dermis; *d.sw.g.*, duct of sweat gland; *der.*, dermis or corium; *epid.*, epidermis; *h.l.*, stratum corneum or horny layer of the same; *hr.*, hair; *mus.*, muscles by which the hair may be made to stand on end; *M.L.*, Malpighian layer; *pap.*, hair papilla; *sb.g.*, sebaceous gland; *sw.g.*, sweat gland.

covered with a stratified epidermis. There are no scales, but cellular outgrowths of the epidermis form hairs, which are peculiar to the warm-blooded, suckling animals known as *Mammalia*. Each hair is embedded in a pit or follicle of the epidermis, at the bottom of which it arises by the growth of the epidermic cells which cover a vascular papilla. The bristles of the crayfish or of hairy caterpillars, and the setæ of the earthworm, are not true hairs, but cuticular structures secreted by the epidermis. The skin also contains sweat or sudorific glands and grease or sebaceous glands which

**General
Anatomy and
Skin.**

secrete an oily substance into the hair follicles. The glands and follicles are parts of the epidermis, but project inwards into the dermis. Below the latter is a layer of fatty tissue. The muscles of the adult rabbit, as in the frog, show little trace of the segmentation which they have in the early stages of development. The general arrangement of the internal organs resembles that of the frog, but a muscular partition, the *midriff or diaphragm*, separates off from the abdominal cavity a *chest or thorax* in the breast region, in which the pericardium lies in the middle, with on each side a *pleural cavity*, into which the lung of its side projects. Between the pleural cavities is a space with membranous walls, known as the *mediastinum*, in which lie the pericardium, gullet, and certain of the great blood vessels.

The skeleton of the rabbit in its main features, and to a considerable extent in its details, resembles that of the frog, but only in its broadest outlines can a correspondence with that of the dogfish be traced. It is almost entirely bony, though most of it is first laid down in cartilage, which persists upon the surfaces of the joints and elsewhere. The vertebræ¹ are much like those of the frog (p. 26), each of them being entirely bony and consisting of a body or centrum with two neural arches, which enclose above the centrum a vertebral foramen, surmounted by a neural spine. As in the frog, each arch bears in front an upward-facing facet or prezygapophysis and behind a downward-facing postzygapophysis, which fits on to the corresponding prezygapophysis of the next vertebra, while at each end there is an intervertebral notch for the passage of a spinal nerve and at the side a transverse process projects. Each end of each centrum, with the exception of the first, is flat, and has applied to it in the young rabbit a thin bony disc or *epiphysis* which fuses with it when growth is complete. There is more difference between the vertebræ than in the frog, the backbone being divided into five sections, the neck or cervical, chest or thoracic, loin or lumbar, hip or sacral, and tail or caudal regions. In the *cervical region* there are seven vertebræ, which may be recognised by the fact that each of the trans-

¹ The general characters of the vertebræ of the rabbit may be well studied in that known as the second lumbar (see below).

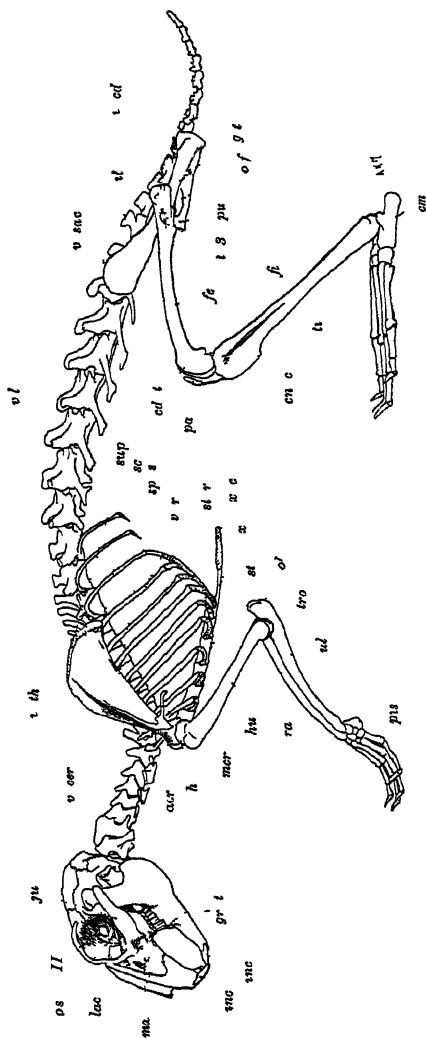


FIG 231 —The skeleton of a rabbit

ac21, Acromion *cd t*, condyles for ulna *cm*, calcaneus, *cu c*, cnemial crest, *fe*, shaft of femur, *fi*, fibula, *s*, *t* great trochanter *gr t*, premoiai and molar teeth *h*, head of humerus, *hu*, shaft of humerus, *il*, ilium, *inc*, upper incisor teeth of the left side *inc*, lower incisor tooth *is* ischium *ju* jugal bone *mer*, metacarpion *mc*, maxilla, *o f*, obturator foramen, *ol* olecranon process *os*, orbitosphenoid bone *pa*, knee cap, *pis*, pisiform bone *pu*, pubis *ra*, radius, *sc*, scapula, *sp s*, spine of scapula *st*, sternum *st r*, sternal ribs, *sub*, suprascapular *t* 3 third trochanter *ts* tibia *to* trochlea *ul*, ulna *v* *cd*, *ver*, *ε*, *l*, *vac*, *o th*, caudal, cervical, lumbar, sacral, and thoracic regions of the backbone, *v r*, vertebral ribs, *z*, xiphisternum *z c*, xiphoid cartilage, *zl*, foamen for optic nerve The clavicle and hyoid are not shown For the parts of the feet, breastbone, and skull which are not lettered here, see Figs 233-240

verse processes is pierced by an opening, known as its *foramen*, through which the vertebral artery passes, so that there is formed an interrupted *vertebrarterial canal* on each side. This is due to the fusion with the vertebræ of short cervical

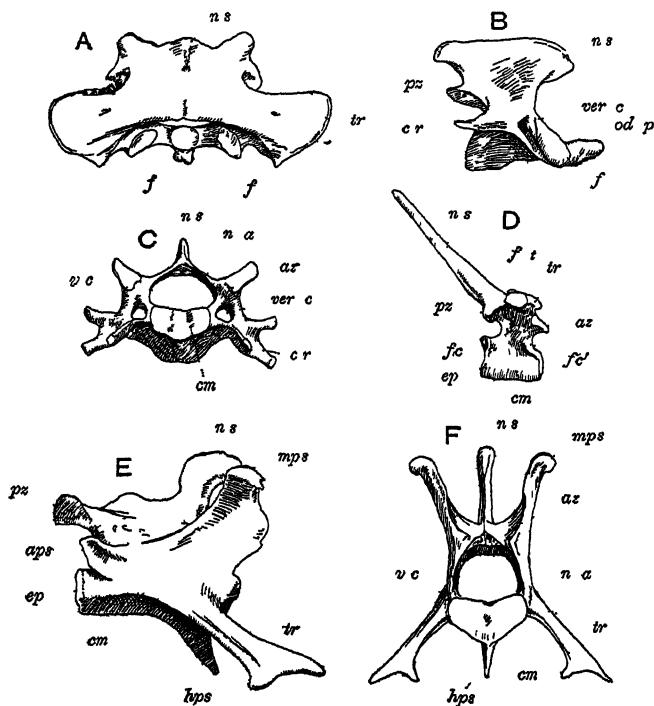


FIG. 232 —Vertebrae of a rabbit

A Atlas from above B, axis from the right C, one of the middle cervical vertebrae, from in front D fourth thoracic vertebra from the right, E second lumbar vertebra, from the right F, the same from in front

aps, Anapophysis, az, prezygapophysis, cm, centrum, cr, cervical rib, ep, epiphysis, f, facet on axis for articulation with atlas f, corresponding facet on atlas f, facet on atlas for odontoid process fc fc demifacets for heads of ribs ft facet for tuberculum hps hypophysis mps, metaphysis na neural arch, ns neural spine od p, odontoid process pz, postzygapophysis tr, transverse process vc, vertebral foramen, ver c, foramen of transverse process

ribs in such a way as to constitute a compound transverse process which encloses a space. The first vertebra, known as the *atlas*, is ring-shaped, with a very large vertebral foramen and no centrum. The ring is divided by a ligament into an upper part, through which the spinal cord passes, and a lower part, into which fits a peg, known as the *odontoid process*, projecting forward from the centrum of the second vertebra. This peg represents the centrum of the atlas removed from it and fused with the vertebra behind. The transverse processes of the atlas are very broad, and the front side of the vertebra has two very large articular surfaces for the occipital condyles. The second vertebra is known as the *axis* or *epistropheus*. It has a long, crest-like neural spine and bears the odontoid process. The remaining cervical vertebrae are short and broad, with low neural spines, except that of the seventh. The *thoracic region* contains twelve or thirteen vertebrae, which are characterised by bearing movably articulated ribs. The neural spines are long, the transverse processes short and stout, and each, in the first nine vertebrae, provided on the under side with a facet or "costal pit" for articulation with the tubercle of a rib. The front end of the centrum (in the first six the hinder end also) bears on each side a facet for the head of the rib. The hinder vertebrae of this set gradually become more like those of the *lumbar region*. These are usually seven in number. They are characterised by their large size and the great development of their processes, the *prezygapophysis* being borne upon the inner side of a large *metapophysis* and the hinder intervertebral notch being overhung by a small *anapophysis*. In the first two the centrum bears a median ventral *hyapophysis*. The lumbar vertebrae have no ribs. There is usually only one *sacral vertebra*, but sometimes two are found. These vertebrae are large and bear at the sides a pair of wing-like expansions, which support the hip girdle and are probably ribs fused with the vertebra. A certain number of the succeeding vertebrae are fused with the true sacral vertebra, the whole mass being known as the *sacrum*. The *caudal region* contains about eighteen vertebrae, of which the first three or four are fused with the sacral. They grow smaller from before backwards, losing their processes and becoming degenerate.

The *ribs* are present as independent elements only in the thoracic region. They are curved, bony rods, articulated with the vertebræ. Those of the first nine pairs are connected at their lower ends with the breastbone by bars of calcified cartilage known

Ribs and Breastbone.

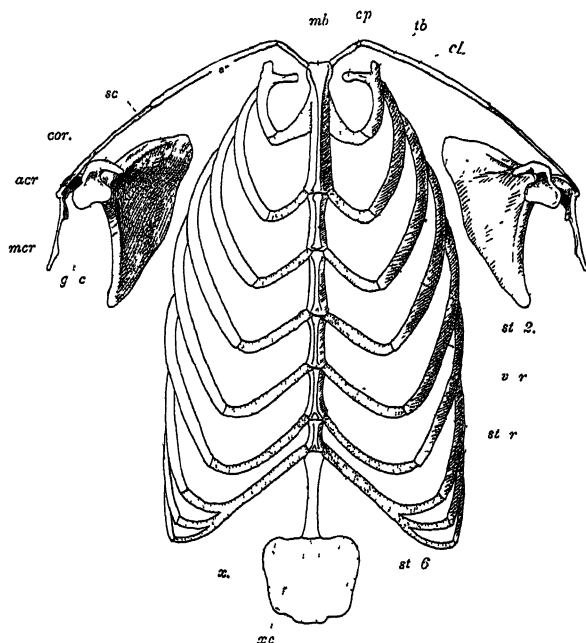


FIG. 233.—The breastbone and shoulder girdle of a rabbit, seen from below and somewhat from in front.

acr., Acromion; *cl.*, clavicle; *cor.*, coracoid process; *cp.*, capitulum; *g.c.*, glenoid cavity; *mb.*, manubrium; *mcr.*, metacromion; *sc.*, scapula; *st. 2*, sternal portion of a rib; *st. 2*, *st. 6*, second and sixth sternbræ; *tb.*, tuberculum; *v.r.*, vertebral portion of a rib; *x.*, xiphisternum; *x.c.*, xiphoid cartilage.

as their *sternal portions* or as *sternal ribs*. The end which articulates with the vertebra has a knob known as the *head or capitulum*. The first nine pairs have a second facet, known as the *tuberculum*, on the dorsal side at a short distance

beyond the head. This is for articulation with the transverse process of the vertebra, and immediately beyond it is a short projection for the attachment of ligaments. The sternal portions of the first seven pairs articulate directly with the sternum; those of the eighth and ninth are connected with the ribs in front of them. The last three pairs have no sternal portions and no tubercula. The breastbone or sternum is a long, narrow rod in the mid-ventral line of the thorax divided into segments. The first segment is the *manubrium*. It is the largest and is flattened from side to side. Behind it come four segments of equal size, then a very short segment, and finally the *xiphoid process or xiphisternum*, a long, slender rod, which bears behind a horizontal plate of cartilage. The ribs of the first pair articulate with the sides of the manubrium and the succeeding six pairs between the segments.

The skull¹ contains the same regions that we have met with in the frog and dogfish, but it consists practically entirely of bones, which meet one another by jagged *sutures*.

The cranium or brain-case proper is relatively short, lies almost wholly behind the orbits, and is not in a line with the facial region, which is bent downwards at an angle of 60° upon it. Its bones are arranged in a series of three rings. (1) The *hinder or occipital ring* consists of four cartilage bones (p. 29). The *basioccipital* is a flat bone which forms the floor of the ring, including the lower edge of the foramen magnum and a small part of each occipital condyle. The *exoccipitals* make the sides of the ring, bounding the foramen laterally and forming the greater part of the condyles. The *supraoccipital* is a large median bone which roofs the occipital ring. (2) In the *middle or parietal ring* there are both cartilage and membrane bones. It abuts on the occipital ring above and below, but at the sides is separated from it by the auditory capsules and squamosal bone. The floor of the cranium in this region is formed by a cartilage bone known as the *basisphenoid*, which lies in front of the basioccipital. It is triangular with the apex truncated and placed forwards, and upon its upper surface is a hollow which lodges the pituitary body. The *alisphenoids* are a pair of irregular cartilage bones which lie at the sides of the basisphenoid and form the lower part of the lateral wall of the cranium. The *parietals* are two large, square membrane bones upon the roof of the cranium, separated

¹ The skull of the dog is in some respects a more suitable example than that of the rabbit for the preliminary study of a mammalian skull. Good accounts of it may be found in Flower's *Osteology of the Mammalia*, Reynold's *Vertebrate Skeleton*, and other works.

at the sides from the alisphenoids by the squamosals. The parietals meet in the middle line. Behind there is wedged in between them and the supraoccipital a small median *interparietal*. (3) The *foremost or frontal ring* contains a narrow median ventral cartilage bone known as the *presphenoid*, which lies in front of the basisphenoid and is connected with it by cartilage. With the presphenoid are fused at the sides a pair of cartilage bones known as the *orbitosphenoids*, which form the lower part of the lateral walls of the cranium in the orbital region. Above them the *frontals*, a pair of large oblong membrane bones, complete the side walls and form the roof, each bearing a large *supraorbital ridge*. (4) The front wall of the cranium is formed by a

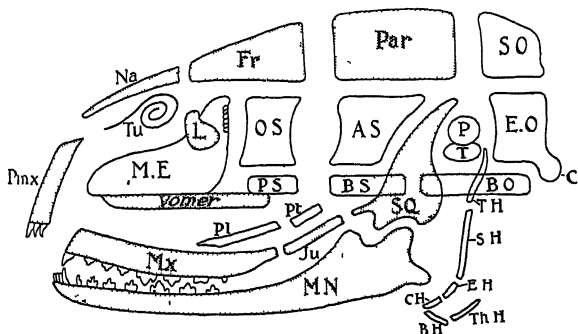


FIG. 234.—A diagram of the skull bones of a mammal (partly after Flower and Weber), the membrane bones shaded.

BO., Basioccipital; EO., exoccipital; C., condyle; SO, supraoccipital; Par., parietal; Fr, frontal, Na., nasal; Pmx., premaxilla; ME., mesethmoid; L., lachrymal; Tu., turbinal; PS., presphenoid; OS., orbitosphenoid; AS., alisphenoid; BS, basisphenoid; SQ., squamosal; P., periotic; T., tympanic; Pl, palatine; Pt., pterygoid; Mx, maxilla; Ju, jugal; T.H., tympanohyal; S.H., stylohyal; E.H., epihyal; CH., ceratohyal, BH., basihyal; Th.H., thyrohyal; vomer; MN., mandible.

partition of cartilage bone, known as the *cribriform plate*, pierced by a number of holes, through which the olfactory nerves pass to the nasal capsules.

We have seen that the occipital and parietal rings are separated on each side of the cranium by a gap, in which stand the auditory capsule and *squamosal*. The latter is a large membrane bone which abuts on the parietal, frontal, alisphenoid, and orbitosphenoid. From its outer surface there arises a stout *zygomatic process*, which bears on its under side the fossa for the articulation of the lower jaw and, beyond the facet, bends downwards to join another bone, the jugal, presently to be mentioned, thus forming the *zygomatic arch or cheek-bone*. From the hinder border of the squamosal a slender *post-tympanic process* extends backwards. The auditory capsule consists of a large cartilage bone,

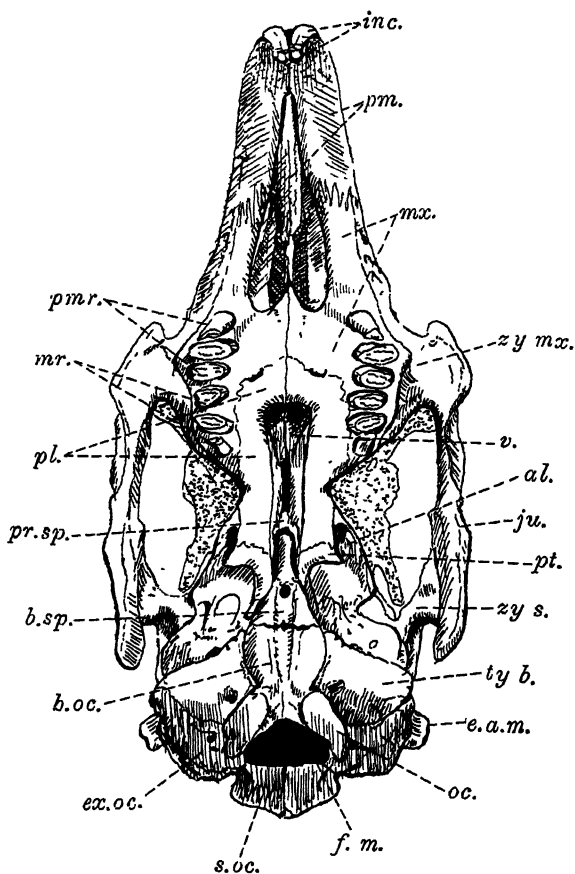


FIG. 235.—A ventral view of the skull of a rabbit.

al., External process of the alisphenoid; *b.oc.*, basioccipital; *b.sp.*, basisphenoid; *e.a.m.*, external auditory meatus; *ex.oc.*, exoccipital; *f.m.*, foramen magnum; *inc.*, incisors; *ju.*, jugal; *mr.*, molars; *mx.*, maxilla; *oc.*, occipital condyle; *pl.*, palatine; *pm.*, premaxilla; *pmr.*, premolars; *pr.sp.*, presphenoid; *pt.*, pterygoid; *s.oc.*, supraoccipital; *ty.b.*, tympanic bulla; *v.*, vomer; *zy.mx.*, zygomatic process of maxilla; *zy.s.*, zygomatic process of squamosal.

known as the *petrotic*, which ossifies in development from three centres, one of which represents the *prootic*. This bone fits loosely into a gap between the squamosal and the exoccipital. Its inner part is dense and known as the *petrous portion*, this encloses the auditory labyrinth. The outer part, which shows on the surface of the skull, is the *mastoid portion*. Against the lower part of the petrotic is placed a thin membrane bone shaped like a flask with a gap on one side, the gap being turned towards the petrotic. This is the *tympanic bone*. The body of the flask, or *bulla*, encloses the tympanic cavity, and the neck leads upwards and outwards from the drum to the ear opening, the passage it encloses being known as the *meatus auditorius externus*. At its inner end is a ring which marks the position of the drum in life.

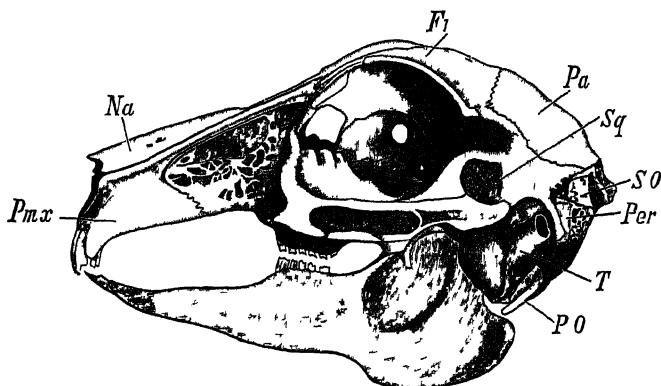


FIG 236 —A side view of a rabbit's skull —From Thomson

Pmx, Premaxilla *Na*, nasal *Fr*, frontal *Pa*, parietal *Sq*, squamosal *SO* supraoccipital *Per*, petrotic *T*, tympanic (the reference line points to the bony external auditory meatus, beneath it lies the inflated bulla) *PO*, paroccipital process

The inner wall of the tympanic cavity is formed by the petrotic bone, and on it may be seen two gaps, the *fenestra ovalis* and behind it the *fenestra rotunda*. In life a chain of three little cartilage bones, the *malleus*, *incus*, and *stapes*, connect the fenestra ovalis with the drum in the same way as the columella auris of the frog. These bones belong in reality to the visceral arches.

The part of the skull in front of the cranium is known as the *facial region*. It consists of the nasal capsules and certain of the bones of the upper jaw, and we have seen that it is bent downwards at an angle of 60° with the cranium. The *nasals* are elongated membrane bones which form the roof of the nasal cavities, uniting by a suture with the frontals behind. The *mesethmoid* is a median vertical plate of cartilage extending forward from the cribriform plate and separating

the nasal cavities. The *vomers* are a pair of slender, blade-like bones, fused with one another along their lower edges, which enclose between them the lower edge of the mesethmoid cartilage and strengthen and complete the internasal septum. Behind they send out flanges or "wings" towards the sides of the nasal cavity, so as to form a horizontal partition, which separates an upper olfactory chamber from a lower narial passage. The outer sides and floor of the nasal cavities are formed by the palatines, maxillæ, and premaxillæ presently to be mentioned. The surface of the cavities is increased by three pairs of

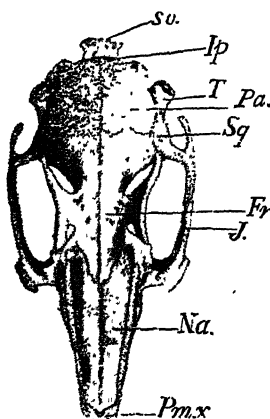


FIG. 237.—A dorsal view of a rabbit's skull.—From Thomson.

SO., Top of supraoccipital, Ip., interparietal; T., tympanic; Pa., parietal; Sq., squamosal; Fr., frontal; J., jugal; Na., nasal; Pm.x., premaxilla.

thin and much-folded plates of cartilage bone known as the *turbinals* which project into them from their walls. In the upper jaw there may be recognised the same two series of bones as in the frog, the bones being membrane bones. The *pterygoids* are two vertical plates of bone attached to the lower side of the cranium at the junction of the basisphenoid with the alisphenoid bones. The *palatine bones* are a larger pair, which consist each of a vertical portion, attached above to the ventral side of the presphenoid and behind to the pterygoid, and a horizontal portion which meets its fellow in the median plane in the roof of the mouth. There is no quadrate bone. The *premaxillæ* are a pair of bones which form the front of the upper jaw and lodge the upper pair of large gnawing teeth. It has a nasal process, which passes backwards beside the nasal bone, and a palatine process, which, like that of the palatine bone, forms part of the floor of the nasal passages. The *maxillæ* are two large irregular bones which lie behind the premaxillæ in the facial region. The main part of each bears the upper grinding teeth.

From this arises a palatine process, like that of the premaxillæ and palatine bones, which it connects so as to form a floor to the narial passages, and a zygomatic process, which passes outwards and backwards to form the front part of the zygomatic arch. The zygomatic processes of the maxilla and squamosal are joined by a bar of bone known as the *jugal or malar bone or zygoma*. The *lacrymals* are a pair of small bones which form part of the front walls of the orbits, lying between the frontals and maxillæ.

The lower jaw is composed of membrane bone and represents the dentaries of the frog, Meckel's cartilage,

which is present during development, being absent in the adult. The jaw articulates, not with a quadrate cartilage, but with the squamosal bone. The *hyoid bone*, lying in the floor of the hinder part of the mouth, represents that part of the visceral skeleton which does not form the jaws and ear ossicles. It consists of a median body representing the basihyal and two pairs of backwardly projecting cornua, of which the hinder are the larger. The anterior cornua represent the hyoid arches, and are completed by a series of small separate bones, which connect the hyoid bone with the periotic region of the skull. The posterior cornua represent the first pair of branchial arches.

The following openings exist in the wall of each side of the skull:

- (1) The *anterior nares* at the front end of the nasal capsule, for the nostril.
- (2) The *anterior* and (3) the *posterior palatine foramina*, a large and a small opening in the palate for the passage of branches of the maxillary nerve and blood vessels between the palate and the nasal cavity.
- (4) The *lacrimal foramen* between the lacrimal and maxillary bones, for the lacrimal duct which conveys tears into the nose.
- (5) The *infraorbital foramen* in front of the zygomatic process of the maxilla, for the passage of a branch of the maxillary nerve from the orbit to the face.

- (6) The *optic foramen*, a large round hole in the orbitosphenoid for the optic nerve.
- (7) The *foramen lacerum anterius* or *sphenoidal fissure*, a vertical slit between the basisphenoid and alisphenoids for the third, fourth, sixth, and ophthalmic and maxillary branches of the fifth nerves. In most mammals the last-named branch passes through a separate opening, the *foramen rotundum*.
- (8) The *foramen lacerum medium*, an irregular opening on the under side of the skull between the alisphenoid and the periotic. Its anterior part represents the foramen ovale of other mammals and transmits the mandibular branch of the fifth nerve.
- (9) The *stylomastoid foramen*, a small opening behind the tympanic, through which the seventh nerve leaves the skull.
- (10) The *foramen lacerum posterius*, an irregular opening on the under side of the skull, between the occipital condyle and the tympanic bulla, through which the ninth, tenth, and eleventh nerves and the internal jugular vein pass.
- (11) The *carotid foramen*, which pierces the tympanic bone near its inner border, close to the occipital condyle, and transmits the internal carotid artery.
- (12) The *condylar foramina*, a couple of holes in the exoccipital, just in front of the condyle, through which the

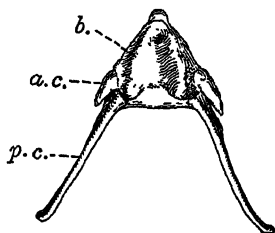


FIG. 238.—The hyoid bone of a rabbit, from above.

a c., Base of the anterior cornu; *b.*, body; *p c.*, posterior cornu.

hypoglossal nerve passes in two divisions. In connection with the tympanic cavity there are two openings, the *Eustachian canal* at the anterior and inner angle of the tympanic bone, on the under side of the skull, behind the foramen lacerum medium, and the *external auditory aperture* at the end of the neck or spout of the tympanic flask.

The shoulder girdle practically consists of one bone, the scapula, on each side. This is a flat, triangular structure, with the apex downwards

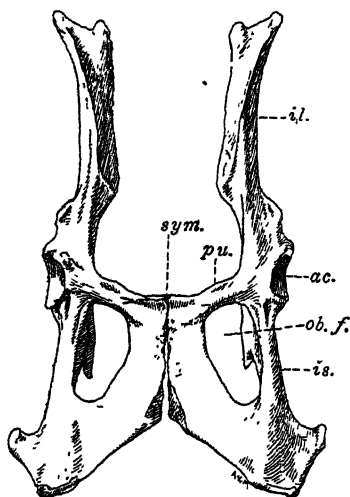


FIG. 239.—The pelvic girdle of a rabbit, from beneath.

ac., Acetabulum; il, ilium, is, ischium; ob f, obturator foramen; pu., pubis; sym, symphysis pubis.

Fore-limb. and forwards,

bears a prominent external ridge or *spine*, which at its lower end becomes free as an acromion with a long backward *metacromion*. At the apex is the shallow glenoid cavity for the humerus, in front of which a small hook or *coracoid process* represents the coracoid bone of the frog. Along the convex dorsal border lies a narrow cartilaginous suprascapula. The clavicle is a slender, curved bone, lying in a ligament between the acromion and the sternum. In mammals which move the forearm freely, as in man, it is well developed

and articulates with acromion and sternum.

The hip girdle is large, and each of its halves is known as an *os innominatum*. With the sacrum it forms a ring known as the *pelvis*. In each *os innominatum* may be recognised a large dorsal ilium articulated with the sacrum, a posterior ischium, and a smaller ventral and anterior pubis which unites with its fellow in a symphysis. The ischium and pubis are separated by a large *obturator foramen*, above and

below which they meet. Above the obturator foramen all three parts of the os innominatum are continuous around the acetabulum, into which the head of the femur fits.

The limbs contain the same bones as in the frog. In the fore-limb the humerus has in front of the head a *bicipital groove* for the tendon of the biceps muscle, bounded by two roughened projections, on the inner side the *lesser tuberosity or small tubercle*, and on the outer side the *greater tuberosity or large tubercle*. At the lower end is a pulley-like trochlea, above which is the *supratrochlear fossa* in front and the *olecranon fossa* behind, a *supratrochlear foramen* putting the two fossæ into communication. In the forearm the radius and ulna are distinct but not movable upon one another, the radius lying in front of the ulna. In man the lower end of the radius rotates round the ulna, so that the former lies in front of and obliquely across the latter when the palm faces downwards, but parallel with and outside it when the palm is turned upwards. The position in which the palm is downwards is known as *pronation*, that in which it is upwards as *supination*. In the frog the limb is fixed half-way towards pronation; in the rabbit it is fixed in the prone position. A large olecranon process of the ulna fits into the olecranon fossa. In the wrist all the nine bones of the typical plan are present, arranged, as usual, in a proximal and a distal row with a *central bone or centrale* between them. In the proximal row of three bones the radial is known as the *scaphoid*, the intermediate as the *semilunar or lunate*, and the ulnar as the *cuneiform or os triquetrum*. In the distal row there are four distal carpals, the first on the inner side being known as the *trapezium*, the second as the *trapezoid*, the third as the *os magnum or capitatum*, and the fourth, which represents two fused, as the *unciform or os hamatum*. On the hinder side of the wrist is a small *pisiform* bone. There are five digits, of which the first is the shortest and the third the longest. In the hind-limb, the femur has a prominent head, below which are three rough prominences, the *greater trochanter* on the outside, the *lesser trochanter* on the inner side, and the *third trochanter* below the great trochanter. At the lower end of the bone are two large condyles for the tibia.

A *knee-cap* or *patella* covers the knee joint and is connected by ligament with the tibia. The tibia and fibula are fused at their lower ends only. The latter is a small splint of bone outside the former, which is straight and stout and bears in front a prominent *cnemial crest*. In the ankle the

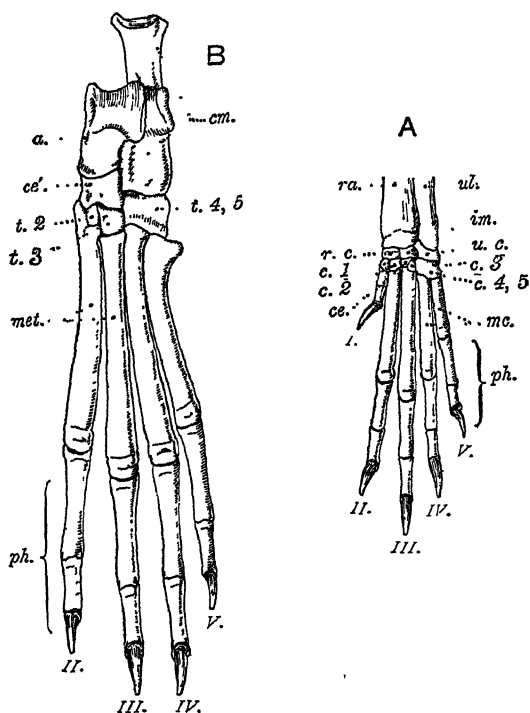


FIG. 240.—The skeleton of the left fore- and hind-feet of a rabbit.

A, fore-foot; B, hind-foot.

- a., Astragalus; c. 1, first distal carpal or trapezium; c. 2, second distal carpal or trapezoid; c. 3, third distal carpal or magnum; c. 4, 5, fused fourth and fifth distal carpals or unciform; ce., centrale; ce', centrale of hind-foot or navicular; cm., fibulare or calcaneus; im., intermedium or semilunar; mc., metacarpals; met., metatarsals; ph., phalanges; ra., lower end of radius with its epiphysis; r.c., radiale or scaphoid; t. 2, second distal tarsal or mesocuneiform; t. 3, third distal tarsal or ectocuneiform; t. 4, 5, fused fourth and fifth distal tarsals or cuboid; u.c., ulnare or cuneiform; ul., lower end of ulnar with its epiphysis; I.-V., digits.

bones, like those of the wrist, are arranged in two rows with a central bone between them. The first row contains, as in the frog, two bones, the astragalus, which corresponds to a fused tibiale and intermedium, and the fibulare or calcaneus, which lies outside the astragalus and projects backwards to form the heel. The distal row consists of three bones, that which corresponds to the missing first digit being absent, and those which correspond to the outer two digits being fused together. The innermost of the remaining bones of the row is known as the *meso-cuneiform*, the next as the *ectocuneiform*, and the third as the *cuboid*. The metatarsals are long and there are four digits.

The mouth differs from that of the frog in the possession of a *palate*—an inner roof which separates from the mouth a *narial passage*. By this passage the approach from the nostrils to the mouth is prolonged backwards, so that the internal nares open into the pharynx instead of into the forepart of the mouth (Fig. 241). The first part of the inner roof is strengthened by the horizontal processes of the premaxillary, maxillary, and palatine bones and is known as the *hard palate*; the hinder part is purely fleshy and is known as the *soft palate*. The narial passage lies above the palate and below the true olfactory chambers, from which it is separated behind by a partition, supported by the vomer, representing the true roof of the mouth. In the front part, however, the true roof is wanting and the narial passage is continuous with the olfactory chamber. In this part the passage is double, behind it is single. Into the hinder part open the Eustachian tubes. The *tonsils* are a pair of pits at the sides of the soft palate near its hind border. The tongue is an elongate, muscular mass attached along most of its length to the floor of the mouth, but with a free tip in front. It bears papillæ of several kinds which subserve the sense of taste. The teeth differ from those of the dogfish and frog in that (1) they are not all alike, (2) they are inserted in sockets in the jaw, whereas those of the dogfish are embedded in the skin and those of the frog are fused to the jaw, (3) they are borne on the edges of the jaws only,

**Alimentary
System :
Mouth, Teeth,
and Pharynx.**

and not on the roof of the mouth like the vomerine teeth of the frog, (4) instead of being continually replaced by the upgrowth of skin from a groove as in the dogfish, or one by one as in the frog, they are in two definite sets, the *milk teeth* and the *permanent teeth*, of which the first is lost at

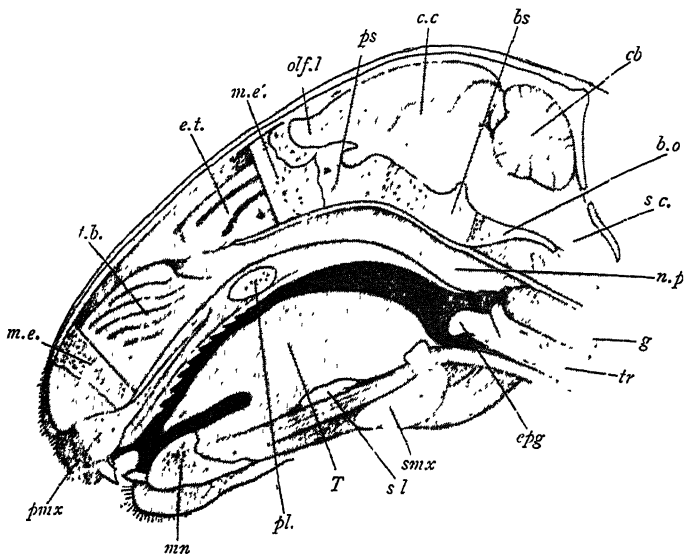


FIG. 241.—A vertical section through a rabbit's head.—From Thomson.

p.m.x, Premaxilla with incisors; *m.e.*, part of mesethmoid in front region, where nasal passage is not separate; *m.e'*, part of same in hinder region (the intermediate part is cut away); *e.t.*, maxillary turbinates; *olf.l.*, olfactory lobe of cerebrum; *ps.*, presphenoid; *c.c.*, position of corpus callosum; *bs.*, basisphenoid with depression for pituitary body; *cb.*, cerebellum; *b.o.*, basioccipital; *s.c.*, spinal cord; *n.p.*, nasal passage; *g.*, gullet; *tr.*, trachea; *epg.*, epiglottis; *smx.*, submaxillary salivary gland; *s.l.*, sublingual salivary gland; *pl.*, transverse portion of palatine; *mn.*, anterior end of mandible.

an early age and replaced for life by the second. The teeth do not form a continuous series as in man, but the front teeth are separated from the grinding teeth by a wide gap or *diastema*, in the position in which the canine or dog teeth should stand, these teeth, with others, being absent from the rabbit. In the upper jaw the *front teeth* or *incisors* number two pairs, the first pair being long,

curved, and chisel-shaped and the second pair small and hidden behind the first. Unlike the rest of the teeth, and unlike the front teeth of most animals, the incisors of the rabbit do not cease to grow when they have reached a certain size, but continue to add to their bases as fast as they are ground down at the top. The six pairs of grinding teeth are all much alike in appearance, having broad, ridged tops, but they are divided into two sets by the fact that the first three, known as *premolars*, are preceded by milk teeth, while the last three, known as *molars*, are not. In the lower jaw there is only one pair of incisors, these being shaped like the first pair above, with which they work in gnawing off the food which is munched fine by the grinders. There are two pairs of premolars and three pairs of molars. It is usual to express the number and arrangement of the teeth of mammals by a *dental formula*. Thus, in the pig, which has a typical set

of teeth, the formula is $i \frac{3}{3} c \frac{1}{1} pm \frac{4}{4} m \frac{3}{3}$, giving 22 on each side of the mouth, or 44 in all. With this we may compare the dentition of the rabbit, which is $i \frac{2}{1} c \frac{0}{0} pm \frac{3}{2} m \frac{3}{3}$,

the total for both sides being 28. Four pairs of *salivary glands* pour their secretion into the mouth. The *parotid gland* of each side lies behind the angle of the jaw, the *submaxillary gland* lies against its fellow between the angles of the jaw, the *infraorbital gland* lies below the eye behind the cheek-bone, the *sublingual gland* lies along the inside of the mandible. The saliva moistens the food and contains an enzyme, known as *ptyalin*, which turns starch into sugar. The pharynx receives in front the nasal passage and the mouth. Behind, it leads into the gullet above and bears below the glottis, which lies shortly behind the tongue, covered by a flap known as the *epiglottis* which is stiffened by a cartilage. Thus in the pharynx there cross one another the passages by which the food passes to the alimentary canal and the air to the lungs. The oesophagus runs backwards through the neck and chest above the trachea.

Shortly after passing through the diaphragm, the oesophagus joins the stomach. This is a wide sac, placed

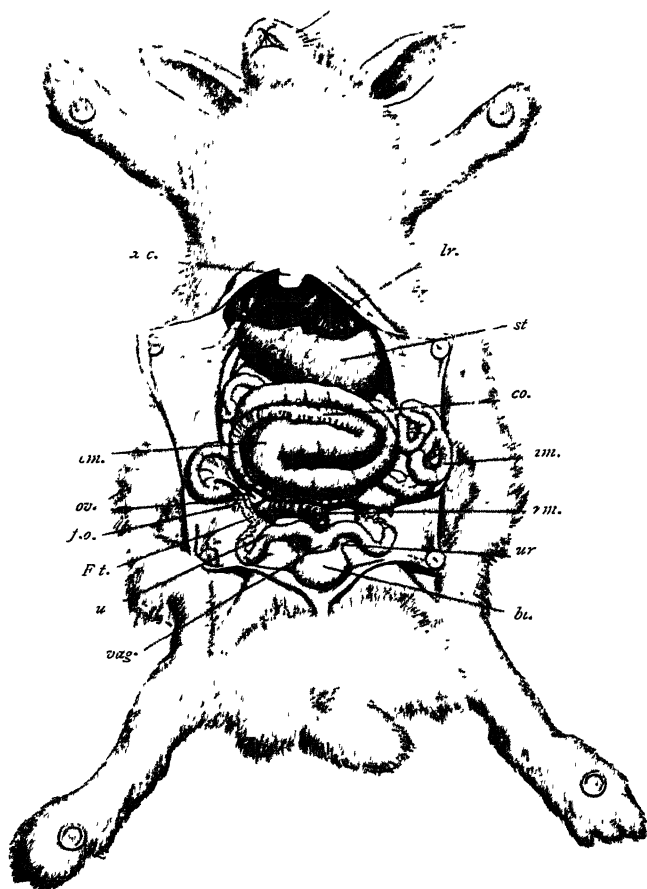


FIG. 242.—The body of a female rabbit with the abdomen opened, the organs being displaced as little as possible.

bl., Bladder; *cm.*, cæcum; *co.*, colon; *F.t.*, Fallopian tube; *f.o.*, fimbriated opening of the oviduct; *im.*, ileum; *lv.*, liver; *ov.*, ovary; *r.m.*, rectum; *st.*, stomach; *ur.*, ureter; *ur.*, right uterus; *vag.*, vagina; *a.c.*, xiphoid cartilage. Note also regions of body (head, neck, chest, abdomen, tail), mouth, nostrils, hare lip, prominent incisor teeth, vibrissæ.

athwart the body cavity and wider at the left or *cardiac end* than at the right or *pyloric end*; it is curved, with the concave side turned forwards, and the oesophagus enters at the bottom of the concavity. The pyloric end communicates with the intestine by a small opening, the *pylorus*, provided with a sphincter. The small intestine is a narrow, much-coiled tube, seven or eight feet in length. Its first section or duodenum runs from the pylorus along the right side of the abdomen nearly to its hinder end and then turns forward again, forming a loop. In the mesentery between the two limbs of the loop lies the thin, diffuse pancreas, whose duct enters the returning limb of the loop about three inches beyond the bend. The liver is a large, dark-red, lobed organ slung from the diaphragm by the falciform ligament; in a groove upon its right central lobe lies the elongated, dark green gall bladder, from which the bile duct runs backwards to open into the dorsal side of the duodenum shortly beyond the pylorus. The remainder of the small intestine is the ileum; it ends in a round swelling known as the *sacculus rotundus*. The lining of the small intestine is beset with numerous minute processes or *villi*, by which its surface is increased. At the junction of the small and large intestine is placed a very large tube, the *blind gut or cæcum*, marked by a spiral constriction and ending blindly in a small, finger-like *vermiform appendix*. The *sacculus rotundus* opens into the cæcum about an inch from the end opposite to the vermiform appendix, the large intestine leaves it at the same end. Two regions

Stomach and Intestine.

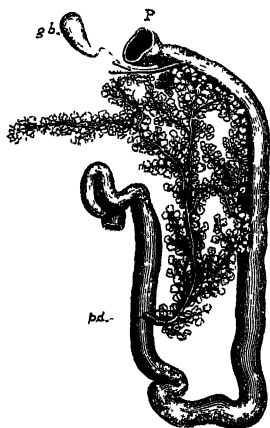


FIG. 243.—The duodenum of a rabbit.—From Krause, in part after Claude Bernard.

P, Pyloric end of stomach; g b., gall bladder with bile duct and hepatic ducts; p d., pancreatic duct

The lining of the small intestine is beset with numerous minute processes or *villi*, by which its surface is increased. At the junction of the small and large intestine is placed a very large tube, the *blind gut or cæcum*, marked by a spiral constriction and ending blindly in a small, finger-like *vermiform appendix*. The *sacculus rotundus* opens into the cæcum about an inch from the end opposite to the vermiform appendix, the large intestine leaves it at the same end. Two regions

may be recognised in the large intestine. The *colon* is a sacculated tube about a foot and a half in length; the rectum is a narrower tube about two and a half feet in length, in which fæcal pellets can be seen.

The spleen is a narrow, crescentic, dark-red body lying close against the convex side of the stomach. The thymus

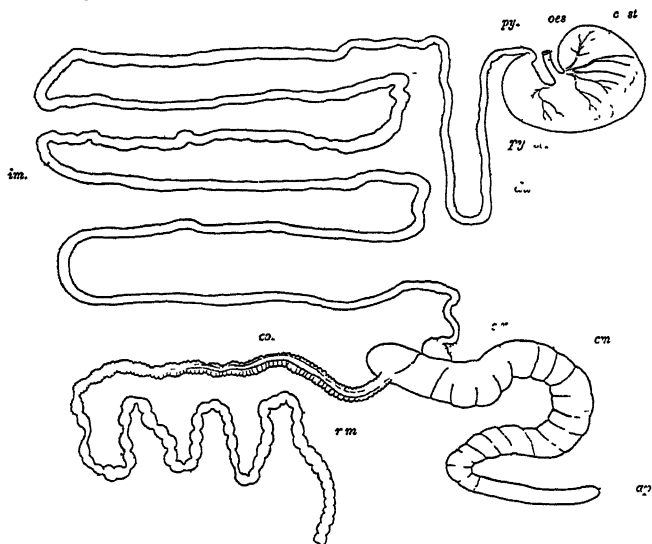


FIG. 244.—The alimentary canal of a rabbit removed from the body and spread out.

ap., Vermiform appendix, *c st.*, cardiac end of stomach; *cm*, cæcum; *co.*, colon; *du.*, duodenum, *im*, ileum; *oes.*, oesophagus, *py.*, pylorus, *py st.*, pyloric end of stomach, *rm*, rectum; *s.r.*, saccus rotundus.

is a soft, pink mass in the mediastinal space at the front of the thorax. The thyroid is a thin, red body consisting of two lobes, one at each side of the larynx, joined by a band across the ventral side of the latter.

Ductless Glands.

The chest or thorax is a closed box whose side walls are formed by the ribs with the muscles between them and its hinder wall by the diaphragm, which divides the main or pleuroperitoneal cœlom, parting two pleural cavities

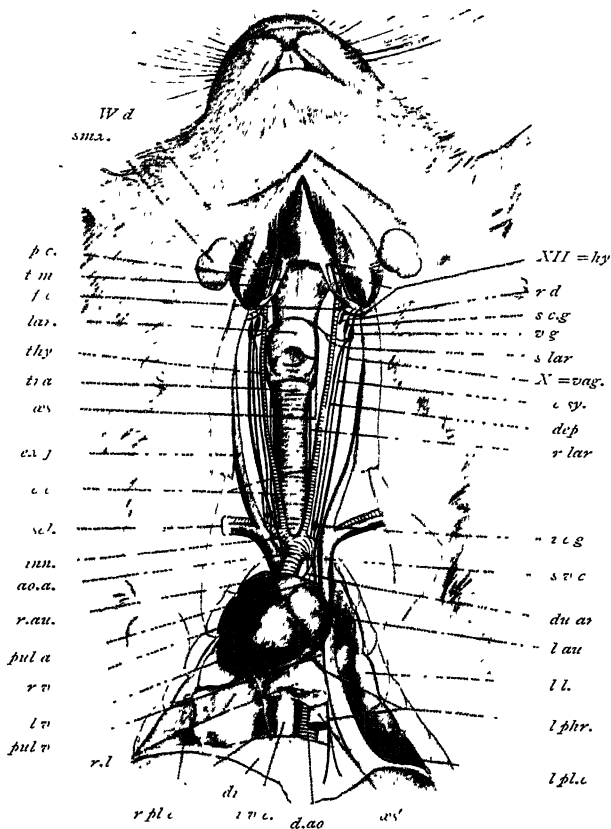


FIG. 245.—A dissection of the neck and thorax of a rabbit. The heart has been displaced a little to the right, and the pericardium removed.

ao.a., Aortic arch, *c.c.*, common carotid arteries; *c.sy.*, cervical sympathetic nerve, *d.ao.*, dorsal aorta; *dep.*, depressor nerve; *di.*, diaphragm; *du.ar.*, ductus arteriosus, *ex.j.*, external jugular vein; *f.c.*, point at which the common carotid divides; *ky.*, hypoglossal nerve; *i.c.g.*, inferior or posterior cervical sympathetic ganglion; *inn.*, innominate artery, *i.v.c.*, inferior vena cava, lying in mediastinum; *lau.*, left auricle, *l.l.*, left lung; *l.phr.*, left phrenic nerve; *l.p.l.c.*, left pleural cavity; *l.v.*, left ventricle; *lar.*, larynx; *as.*, oesophagus in neck; *as'*, the same in mediastinum, *p.c.*, posterior cornu of the hyoid; *pul.a.*, pulmonary artery; *pul.v.*, pulmonary vein, *r.au.*, right auricle, *r.d.*, ramus descendens; *r.l.*, right lung, one part bulging into mediastinum; *r.lar.*, recurrent laryngeal nerve; *r.p.l.c.*, right pleural cavity; *r.v.*, right ventricle; *s.c.g.*, superior cervical sympathetic ganglion; *s.lar.*, superior laryngeal branch of vagus; *s.v.c.*, superior vena cava, *sc.l.*, subclavian artery and vein, *sm.x.*, submaxillary gland; *t.m.*, tendon of mandibular muscle; *thy.*, thyroid gland; *tra.*, trachea; *v.g.*, vagus ganglion; *vag.*, vagus, *XII.d.*, duct of submaxillary gland (Wharton's duct), *X.*, *XII.*, cranial nerves.

in front from a peritoneal cavity behind (p. 335). The windpipe comprises, besides the larynx, a long tube with rings of cartilage in its wall. This is the *trachea* or windpipe proper, which leads back along the neck and in the thorax divides into two bronchi which join the lungs. In these the bronchi break up into numerous *bronchioles*, which end in minute air sacs. The cavity of the thorax is enlarged from back to breast by an outward movement of the ribs and from head to tail by the movement of the diaphragm, which at rest is convex towards the chest, but when it contracts flattens, thus increasing the size of the thorax. Since the pleural cavities are closed, their enlargement tends to set up a vacuum within them, and thus the lungs, which are not closed, expand to fill them, drawing in air¹ through the glottis. The air is driven out by the collapse of the chest owing to the elasticity of the lungs as soon as the muscles of inspiration relax, but this movement can be aided by the contraction of certain other muscles, notably those of the belly, which press the viscera against the diaphragm from behind.

The kidneys of the rabbit are a pair of dark-red bodies, convex on the outer side and concave on the inner, which lie on the dorsal wall of the peritoneal cavity, that on the left side further back than that on the right. Like those of the dogfish and frog they consist of tubules, but they have no nephrostomes. They represent the metanephros only. From the concavity or *hilus* the ureter runs back to open into the bladder. In the early stages of development this organ joins the rectum in a cloaca, but later the latter becomes divided, so that the urinary and generative organs discharge by an independent passage through the vulva or the penis. In front of each kidney lies a small, yellow, suprarenal gland. The testes are a pair of ovoid bodies which arise in the course of development on the dorsal wall of the peritoneal cavity near the kidney, but later become free and pass backward into two pouches of the body-wall at the sides of the penis known as the scrotal

¹ That is, the air enters by its own pressure and expands the lungs when the pressure around them in the pleural cavity is lowered.

sacs. Each testis remains connected with its original position by a *spermatic cord*, which consists of connective tissue with an artery and vein. In passing backwards it carries with it the mesonephros, which in the adult may be seen as a body called the *epididymis* lying along the side of the testis

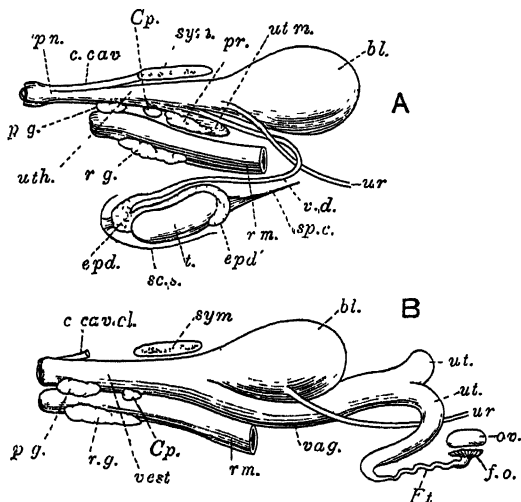


FIG. 246.—The reproductive organs of the rabbit. *A*, male; *B*, female. In each case the dissection is made from the left side, the animal lying on its back.

bl., Bladder; *c. cav.*, corpus cavernosum; *c. cav. cl.*, corpus cavernosum of the clitoris; *Cp.*, Cowper's gland; *epd.*, cauda epididymis; *epd'*, caput epididymis; *f. t.*, Fallopian tube; *f. o.*, fimbriated opening of the same, *ov.*, ovary; *p. g.*, perineal gland; *pn.*, penis; *pr.*, prostate; *r. g.*, rectal gland; *r. m.*, rectum; *sc. s.*, scrotal sac; *sp. c.*, spermatic cord (cut short); *sym.*, symphysis pubis; *t.*, testis; *ur.*, ureter; *ut.*, uterus; *ut m.*, uterus masculinus; *uth.*, urethra; *v. d.*, vas deferens; *vag.*, vagina; *vest.*, vestibule

and enlarged at the front and hind ends into a *caput* and *cauda* respectively. The cauda epididymis is connected to the scrotal sac by a short elastic cord known as the *gubernaculum*. Each epididymis consists of a mass of twisted tubules joining into a single, much-coiled tube which becomes continuous at the cauda with the vas deferens (the Wolffian duct). This passes forwards out of

the scrotal sac, curves over the ureter, and passes backwards again to open into a small median sac known as the *uterus masculinus*, which lies above the neck of the bladder within the pelvic girdle. The uterus masculinus opens into the neck of the bladder, which is known after their junction as the *urinogenital canal or urethra*, and passes backwards into the penis, at the end of which it opens. Beside the uterus masculinus lie the *prostate glands* which pass their secretion into the urethra, and behind the prostate are *Cowper's glands*. The penis is situated behind the symphysis pubis and in front of the anus. It has spongy, vascular walls and is invested by a loose sheath of skin, the *foreskin or prepuce*. The ovaries are small oval bodies attached behind the kidneys to the dorsal abdominal wall, and show on their surface small projections like blisters, known as *Graafian follicles*, each of which contains a microscopic ovum. The oviducts open into the abdominal cavity by wide, funnel-shaped *fimbriated openings* just outside the ovaries. When the ova are ripe the follicles burst and discharge the ova into the funnels which at that time extend over them. The first section of each duct is narrow and gently twisted and is known as the *Fallopian tube*. It runs backwards and enlarges into the *uterus*, a vascular-walled structure which joins its fellow in the middle line in front of the bladder to form the *vagina*. This passes backwards within the pelvic girdle above the neck of the bladder, with which it presently unites to form the *urinogenital canal or vestibule* which opens at the vulva. On its ventral wall lies the small, rod-like clitoris and on the dorsal wall two small Cowper's glands.

During the spring and summer a periodical ripening of ova with their discharge, or *ovulation*, occurs at intervals of about a month. Coition takes place during one of these periods, shortly before ovulation. The spermatozoa travel up the oviducts and fertilisation takes place at the upper ends of the latter. The ova pass down the oviducts, in which they segment. At the end of the third day they reach the uterus. Here at first they lie free. On the eighth day, however, they begin to become attached to the uterine wall, and in the course of the next few days there is formed in connection with each of them a special organ,

known as the *placenta*, in which blood vessels derived from the mother and the developing young lie side by side in very close and extensive contact. Through the thin walls of the two sets of blood vessels interchange of fluid and gaseous contents takes place, and in this way the nutrition and respiration of the young is provided for until birth, which takes place at the end of a month from fertilisation.

The heart of the rabbit lies in the front part of the chest enclosed in the thin pericardium, immediately behind the soft, pink thymus. It has no sinus venosus or conus arteriosus, but there are two ventricles as well as two auricles, so that four chambers are present. Three *venæ cavæ* corresponding to those of the frog open directly into the right auricle, and two pulmonary veins lead by a common opening into the left auricle. The opening from the right auricle into the right ventricle is guarded by a threefold *tricuspid valve* provided with chordæ tendineæ, and a similar twofold *mitral valve* guards the opening between the chambers of the left side. The two sides do not communicate with one another. From the front end of the right ventricle arises the pulmonary artery, and from the left ventricle the *aortic arch* arises in a similar position, but behind the pulmonary artery. The opening of each of these vessels is provided with three semilunar valves. The pulmonary artery divides to supply the two lungs, and the arteries to the head and arms arise from the arch of the aorta, which afterwards supplies the trunk. The auricles contract simultaneously, and the ventricles follow immediately afterwards; then after a short pause the auricles start another contraction. The venous blood which reaches the right auricle from the capillaries of the body is driven by its contraction into the right ventricle and thence in turn through the pulmonary artery to the lungs. Returning oxygenated to the left auricle it is driven into the left ventricle, and thence through the aorta to all parts of the body. There is thus a double circulation, as in the frog, but the separation of the ventricles and connection of the pulmonary artery with one of them and the aorta with the other dispenses with the elaborate apparatus of the truncus arteriosus.

The aortic arch bends over to the left and, as the dorsal

aorta, passes backwards under the backbone through the chest and abdomen, till it becomes the small caudal artery. A ligamentous band, known as the *ductus arteriosus*, connects the aortic arch with the pulmonary artery, just before the bifurcation of the

latter. At one stage in development this band is represented by an open tube. In its course the aorta gives off numerous arteries, of which the following are the most important: (1) The innominate, arising from the top of

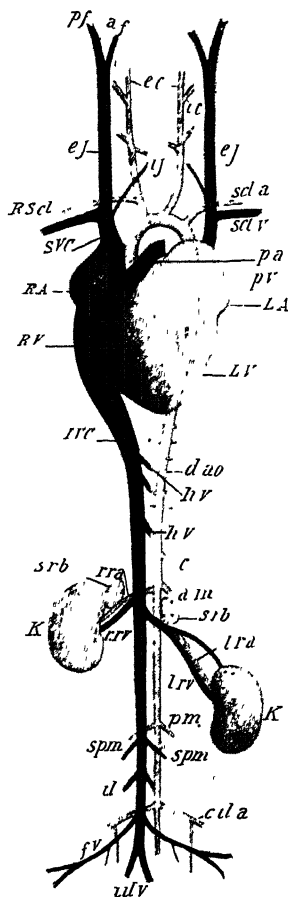


FIG. 247.—The circulatory system of the rabbit.—From Thomson.

(a) Letters to right—

- e.c.* External carotid
- i.c.* Internal carotid.
- e.j.* External jugular
- s.c.l.a.* Subclavian artery
- s.c.l.v.* Subclavian vein.
- p.a.* Pulmonary artery (cut short)
- p.v.* Pulmonary vein.
- L.A.* Left auricle.
- L.V.* Left ventricle
- d.a.o.* Dorsal aorta.
- h.v.* Hepatic veins
- c.* Coeliac artery
- a.m.* Anterior mesenteric.
- s.r.b.* Suprarenal body.
- l.r.a.* Left renal artery.
- l.r.v.* Left renal vein.
- K* Kidney.
- p.m.* Posterior mesenteric artery (incorrectly shown as if paired).
- s.p.m.* Spermatic arteries and veins.
- c.i.l.a.* Common iliac artery.

(b) Letters to left—

- p.f.* and *a.f.* Posterior and anterior facial.
- e.j.* External jugular vein.
- i.j.* Internal jugular.
- R.Scl.* Right subclavian artery.
- S.V.C.* Superior vena cava
- R.A.* Right auricle.
- R.V.* Right ventricle.
- I.V.C.* Inferior vena cava
- r.r.a.* Right renal artery.
- r.r.v.* Right renal vein
- s.r.b.* Suprarenal body
- s.p.m.* Spermatic arteries and veins.
- il* Ilio-lumbar vein
- f.v.* Femoral or external iliac vein
- i.i.v.* Internal iliac veins.

the aortic arch and dividing into the right subclavian and right common carotid, the latter passing up the neck and forking opposite the angle of the jaw into external and internal branches, (2) the left common carotid, arising from the aortic arch immediately beyond the innominate,¹ (3) the left subclavian, arising from the left side of the aortic arch, (4) the coeliac, which arises from the dorsal aorta shortly behind the diaphragm and divides into the hepatic and the lienogastric, (5) the anterior mesenteric, shortly behind the coeliac, (6) the renal arteries, (7) the genital arteries, (8) the small posterior mesenteric, (9) the iliac arteries, which arise just before the hip girdle and practically end the dorsal aorta, which after them is diminished to the caudal artery.

Each superior vena cava is formed by the union of a subclavian vein from the shoulder and fore-limb, an external jugular from the surface of the head, and an internal jugular from the brain. The right superior vena cava receives also an azygos vein from the walls of the chest. The external jugular is larger than the internal and lies nearer the surface in the neck. The inferior vena cava is a large median vessel which lies beside the dorsal aorta. It receives the following veins: (1) The internal iliacs or hypogastrics from the back of the thighs, (2) the external iliacs from the inside of the thighs, (3) the ilio-lumbars from the hinder part of the abdominal walls, (4) the genital veins, (5) the renal veins, (6) the large hepatic veins from the liver, through which organ it passes on its way to the heart. Blood from the stomach, intestines, pancreas, and spleen is carried to the liver by the portal vein, but there is no renal portal system. The lymphatic vessels are gathered up into a *thoracic duct* which opens into the left subclavian vein at its junction with the external jugular. The general course of the circulation in the rabbit is shown in the table on p. 362.

The blood of the rabbit differs from that of the frog and dogfish in two important respects. (1) The red corpuscles, instead of being oval in outline and biconvex, with nuclei, are round and biconcave and have no nuclei. (2) The temperature of the blood, instead

¹ Sometimes from the innominate itself.

of rising and falling with that of the surrounding air or water, is almost constant at about 38°C . This is expressed by saying that the rabbit is a *warm-blooded* animal. The heat is produced, not in the blood, but in the solid tissues, particularly in the glands and muscles, its appearance accompanying the activity of the tissue. The circulation of the blood, however, keeps the temperature of different parts of the body nearly the same. The regulation of the

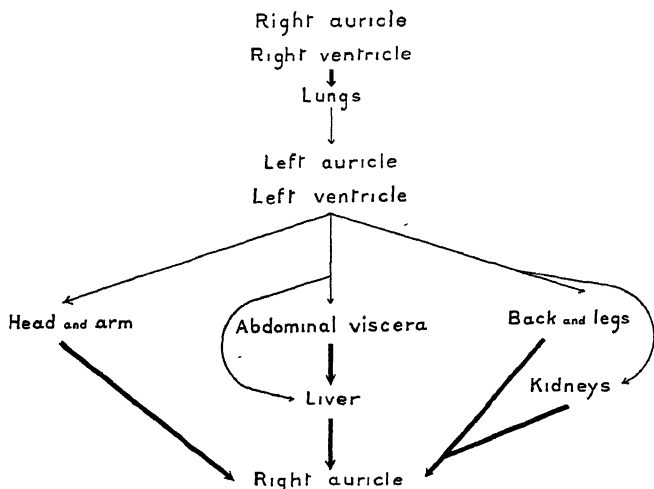


FIG. 248.—A diagram of the circulation of the blood in the rabbit. Thick lines indicate venous blood, narrow lines arterial blood.

temperature of the body as a whole is brought about by alteration in the production of heat and in the rate at which it is lost. The activity of the muscles is the principal means of increasing the production of heat. Shivering is an example of this. Loss of heat is promoted by increased circulation in the skin and by sweating, which absorbs heat in the evaporation of the sweat.

The brain of the rabbit resembles that of the frog in the main outlines of its structure, but there are considerable differences in detail between the two. The most con-

spicuous part is the cerebrum, which consists of two very large cerebral hemispheres divided by a deep cleft or *median fissure*, at the bottom of which they are joined by a bridge known as the *corpus callosum*, composed of nerve fibres, nearly all

Nervous System.

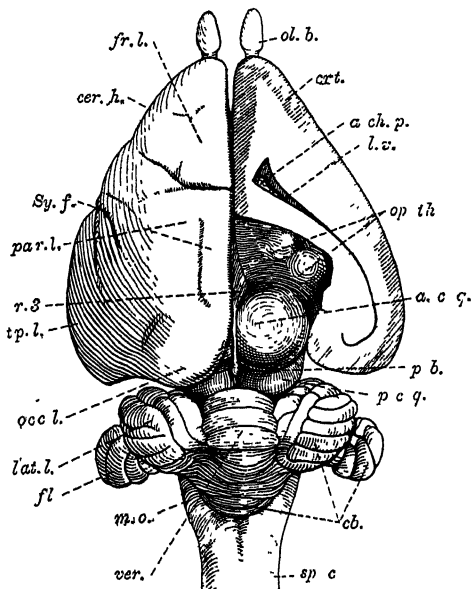


FIG. 249 —The brain of a rabbit, seen from above with part of the right cerebral hemisphere cut away.

a. c. q., Anterior corpus quadrigeminum; *a. ch. p.*, anterior choroid plexus; *cb.*, cerebellum; *cer. h.*, cerebral hemisphere; *crt.*, cortex; *fl.*, flocculus; *fr. l.*, frontal lobe of cerebral hemisphere; *l. v.*, lateral ventricle; *lat. l.*, lateral lobe of cerebellum; *m. o.*, medulla oblongata; *occ. l.*, occipital lobe of cerebral hemisphere; *ol. b.*, olfactory bulb; *op. th.*, optic thalamus; *p. b.*, pineal body; *p. c. q.*, posterior corpus quadrigeminum; *par. l.*, parietal lobe of cerebral hemisphere; *r. 3.*, roof of third ventricle; *sp. c.*, spinal cord; *Sy. f.*, Sylvian fissure; *tp. l.*, temporal lobe of cerebral hemisphere; *ver.*, vermis.

of which run transversely. The surface of the hemispheres is almost smooth, but there can be seen on it faint indications of some of the furrows or *sulci* which in man are deep and numerous and divide the surface into *convolu-*

tions. At about the middle of its length each hemisphere is marked at the side by a shallow groove known as the *lateral or Sylvian fissure*, which separates a *temporal lobe* from the rest. On the under side a longitudinal *rhinal fissure* marks off the *frontal* and *temporal lobes* from a region median to them known as the *rhinencephalon*, which consists of a *hippocampal lobe* behind and the *olfactory lobe* in front. The latter consists of the *olfactory tract* and the *olfactory bulb* which projects in front beyond the frontal lobe. The thalamencephalon is overhung and hidden by the cerebral hemispheres. Its thick sides form two large optic thalami, and from the hinder part of its thin roof the pineal stalk passes backwards to end in the pineal body between the hinder ends of the hemispheres. The infundibulum is a longitudinal depression of the floor of the thalamencephalon, to which is attached the pituitary body. The latter, with the bottom of the infundibulum, is usually torn off in removing the brain from the skull, leaving a longitudinal slit which leads into the third ventricle or cavity of the thalamencephalon. A small, rounded, median swelling immediately behind the infundibulum is known as the *corpus mamillare or corpus albicans*. The mid-brain is almost covered by the cerebral hemispheres. Each of its optic lobes is divided into two by a transverse furrow, so that four *corpora quadrigemina* arise. On its lower side the *crura cerebri* are more prominent than in the frog. In the hind-brain the cerebellum is very large and much-folded and consists of a median lobe or *vermis* and two *lateral lobes*, each of which bears on its outer side a small lobe known as the *floculus*. The lower side of the hind-brain is crossed by a wide, flat band of transverse fibres, the *pons Varolii*, which connects the two halves of the cerebellum. The medulla oblongata is broad in front and narrows gradually backwards to become the spinal cord. It is marked by a *ventral fissure* bordered by two longitudinal bands or *pyramids*.

The cranial nerves are twelve in number. The first ten resemble those of the frog in origin and function, but show certain differences; thus the olfactory nerves arise as a number of fine threads directly from the olfactory bulb and pass at once through the openings of the cribriform plate at

the front end of the cranium, and the seventh nerve has no ophthalmic branch. The *eleventh or accessory nerve* arises from the side of the medulla and spinal cord by a number of roots, the first of which is just behind the vagus and the last at the level of the fifth spinal nerve. It supplies

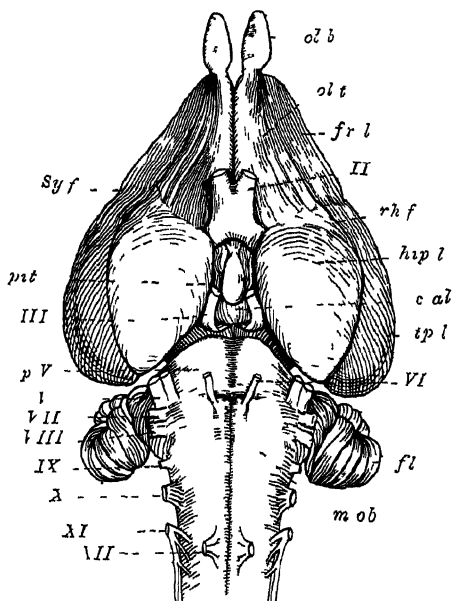


FIG. 250.—The brain of a rabbit from below

c al, Corpus albicans; *fl*, flocculus; *fr l* frontal lobe of the cerebral hemisphere; *hip l*, hippocampal lobe; *m ob* medulla oblongata; *ol b*, olfactory bulb; *ol t* olfactory tract; *p V*, pons; *rh f*, rhinal fissure; *Sy f*, Sylvian fissure; *tp l* temporal lobe of the cerebral hemisphere; *II-XII* roots of the cranial nerves.

certain muscles of the neck. The *twelfth or hypoglossal nerve* also arises by several roots, these are situated on the ventral side of the medulla outside the pyramid. Its course resembles that of the hypoglossal (first spinal) nerve of the frog. The spinal cord and nerves do not differ essentially from those of the frog. The sympathetic system is upon

the same general plan as that of the frog. It has two ganglia on each side in the neck, twelve pairs in the thorax, and the same number in the abdomen. From the hinder thoracic ganglion there starts a *splanchnic nerve*, which passes backwards into the abdomen and ends with its fellow in a *cœliac ganglion* around the anterior mesenteric artery. From this originates an extensive *cœliac plexus*. A number of important nerves belonging to all these series are found in the neck. Among them are the following:

(1) The hypoglossal, curving forwards round the angle of the jaw with a backward branch, known as the *ramus descendens*, which passes to certain of the neck muscles; (2) the vagus, running backwards outside the carotid artery and giving off a *superior laryngeal* branch to the larynx, a *depressor* branch, which arises near the superior laryngeal and passes backwards beside the main vagus, and a

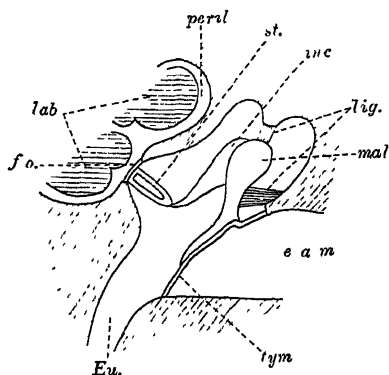


FIG. 251.—A diagram of the ear of a rabbit.

e a m., External auditory meatus; *Eu*, Eustachian tube; *fo.*, fenestra ovalis; *inc*, incus; *lab*, parts of the membranous labyrinth, containing endolymph; *lig*, ligaments; *mal*, malleus; *perl*, perilymph; *st*, stapes; *tym*, tympanic membrane

recurrent laryngeal branch, which loops forward round an artery and runs forwards beside the trachea; behind this the vagus passes backwards along the œsophagus; (3) the *cervical sympathetic*, lying beside the vagus and depressor; (4) the spinal nerves, of which the third gives a *great auricular* branch to the ear and the fourth and fifth give off branches which join to form the *phrenic nerve* to the diaphragm. The vagus bears its vagus ganglion just before it gives off the superior laryngeal nerve, and the sympathetic bears near the ends of the neck its two cervical ganglia. The sense organs do not differ from those of the frog enough to

need special descriptions. Besides the structures we have mentioned in connection with the eye, there must be noticed the *lacrymal glands*, situated above the outer corner of each eye, not below the eye like the corresponding glands in the frog. Their secretion flows over the conjunctiva and passes into the nose by the lacrymal duct at the inner angle. The structures of the outer and middle ear have been mentioned (p. 343). In the inner ear there is present a large, spiral division of the labyrinth, known as the cochlea, which contains the endings of those fibres of the auditory nerve which subserve the sense of hearing. In the nasal cavities (p. 349) the olfactory epithelium is restricted to the upper part of the olfactory chamber, the rest of the organ serving to warm and moisten the air on its way to the lungs. Elaborate taste papillæ of several kinds are found on the tongue.

CHAPTER XXI

MAMMALIA

THE rabbit is a member of a class of backboneed animals which includes man himself, and is on that account usually regarded as the "highest" group in the animal kingdom, though it would be hard to show that they are more highly organised than, for instance, the birds. They are known as Mammals

Mammalia:
Prototheria,
Metatheria,
and Eutheria.



FIG 252.—The Duckmole (*Ornithorhynchus*).—From Thomson.

or *Mammalia* from their possessing milk glands, by which the young are nourished for some time after birth. They are warm-blooded, their skin bears hairs, the heart consists of two auricles and two ventricles and gives rise to a single aortic arch, which curves to the left side, there are two occipital condyles, and the lower jaw articulates with the squamosal bone. One little group of mammals, found in Australia, Tasmania, and New Guinea and known as *Prototheria* or *Monotremata*, differs widely from the rest in

that its members lay large, yolky eggs with shells, like those of reptiles and birds. Their urinary, genital, and anal openings discharge into a common cloaca, and the shoulder girdle has well-developed precoracoids and coracoids which meet the breastbone. The Duckmole (*Ornithorhynchus*) is an example of this group. It is a small, aquatic animal with webbed forefeet and a horny bill, which lives in burrows in river banks in Australia. All other mammals have minute eggs, which are not laid, but undergo a great part of their development within the body of the mother, from which they receive nourishment. They have no cloaca or precoracoids, and the coracoids are small projections of the scapula. Among them the Pouched Mammals, *Metatheria*, or *Marsupialia*, stand apart from the rest. Their young are born in a very immature state and carried by the mother for some time in a pouch under the belly. They have a double vagina, and the anus and urinogenital openings are surrounded by a common sphincter. They are found principally in Australia, where they form almost the whole of the wild mammalian population, including the kangaroos, wombats, etc., but the Opossums of America also belong to this group. The remaining mammals, constituting most of the class, are known as Eutheria.

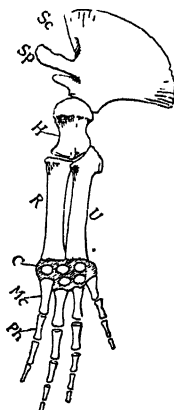


FIG. 253. — The left fore-limb of *Baleenoptera*. — From Thomson.

Sc, Scapula with spine (Sp), H., humerus; R., radius; U., ulna; C, carpals embedded in matrix; Mc, metacarpals; Ph., phalanges.

The most aberrant of the Eutheria are the *Cetacea* or Whales and Dolphins—purely aquatic creatures that live and breed in the water, to which they are conspicuously adapted. Their bodies are fish-like in shape and hairless, save for a few sensory hairs on the head, but are protected by a thick layer of fat, known as the blubber, under the skin. The fore-limbs are replaced by paddles, in which, however, the bones of the

arm and hand can be made out, there are no hind-limbs, the tail bears a pair of fleshy flukes at the sides (not above and below like those of a fish), and in some cases there is a fleshy dorsal fin. The openings of the ears are relatively minute and have no flaps, the eyes are small, and the nostrils are placed at the top of the head. This is in connection with an arrangement by which the end of the soft palate can clasp the epiglottis and form a complete tube from the nostrils to the lungs, so that the animals can feed and breathe at the same time. Thus whales breathe air like all mammals, not water like fish. The so-called spouting of whales is not the driving out of water used in breathing, but partly the getting rid of a little water which has entered the nostrils and mainly the condensation of steam in the breath. Some whales, such as the Sperm Whale, have teeth, which are numerous, simple, and all alike. Others are toothless and provided

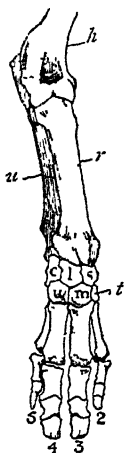


FIG. 254. — The bones of the fore-leg of a pig. — From Thomson.

c., Cuneiform; *h.*, humerus; *l.*, lunar (semilunar or intermedium); *m.*, magnum; *r.*, radius; *s.*, scaphoid; *t.*, trapezoid; *u.*, ulna; 2-5, digits.

with strainers of the horny substance known as "whalebone," by which they obtain for food the countless small creatures which swarm in the surface waters of the sea.

Other aberrant groups of Mammalia, which can only be mentioned here, are the Sea Cows or *Sirenia*, aquatic animals which feed on water plants, and an assemblage of curious creatures known as *Edentata* because their teeth are defective or wanting,

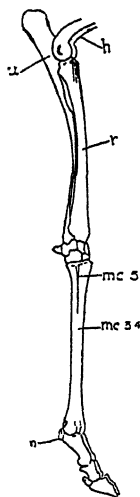


FIG. 255. — The bones of the right fore-leg of a calf, from the outer side. — From Thomson.

h., End of humerus; *mc. 3 4*, cannon bone (fused third and fourth metacarpals); *mc. 5*, fifth metacarpal; *n.*, nodule; *r.*, radius; *u.*, olecranon process of ulna.

Principal Groups of Eutheria.

comprising the Sloths, Armadillos, and Ant-eaters. The rest of the Eutheria fall into three great series: the Hoofed Mammals or *Ungulata*, which are herbivorous; the Nailed Mammals or *Primates*, which in most cases lead an arboreal life and feed upon fruit, eggs, or other food which they find in trees; and a less compact assemblage of groups known as the Clawed Mammals or *Unguiculata*, which are most often carnivorous in one way or another. The broad distinctions between these groups lie in the shape of their feet. The herbivorous ungulates are comparatively defenceless and rely for their preservation from the attacks of carnivorous animals upon their turn of speed, which is attained partly by their walking, not upon the soles of their feet, but upon the tips of their toes, so that the power of their limbs is concentrated. This is expressed by the statement that they are *unguligrade*. Animals which, like dogs and cats, walk upon the under surface of the toes and never place the palm or instep upon the ground are *digitigrade*. Those which, like bears and man, walk upon the whole sole of the foot are said to be *plantigrade*. Those which, like the rabbit, run upon the toes only, but when at rest apply the whole sole to the ground, are *subplantigrade*.

In *Ungulata* the metacarpal and metatarsal bones are lengthened, so that what seems to be "knees" are really the wrist and ankle joints, high above the ground. The first digit is wanting, and usually some of the others are also missing. The ends of those which remain are encased in the broad horny coverings known as hoofs. This does not apply to the elephants, which have five toes with short metacarpals and metatarsals. Hoofs are very broad

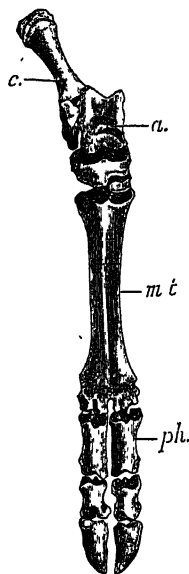


FIG. 256.—The bones of the foot of an ox. —From Thomson.

a, Astragalus; c, calcaneus; m. t., cannon bone (fused third and fourth metatarsals); ph., phalanges.

nails, which cover the sides and part of the ends of the toes. Like other nails, they grow from above downwards. The part which covers the front and side of the last phalanx (the "coffin bone" of the horse) is formed by a thickened ring of skin above it, known as the "coronary cushion." That which covers the end of the digit (the so-called "sole") is formed by the whole surface of the skin it covers. In correspondence with their diet, ungulates have broad grinding teeth, whose surfaces are generally ridged or *lophodont*, though in the omnivorous pigs they are knobbed or *bunodont*. Ungulata fall into three main divisions: those of the even-toed forms or

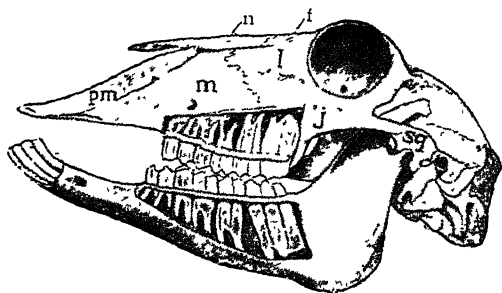


FIG. 257.—A side view of a sheep's skull, with the roots of the back teeth exposed.—From Thomson.

f., Frontal; *n.*, nasal; *pm.*, premaxilla; *m.*, maxilla; *j.*, jugal; *sg.*, squamosal; *l.*, lachrymal

Artiodactyla, comprising the pigs, cattle, antelopes, deer, and camels; the odd-toed forms or *Perissodactyla*, comprising horses, rhinoceroses, and tapirs; and the elephants or *Proboscidea*.

The Artiodactyla are distinguished by the fact that the third and fourth digits of each foot are equally developed, and the line halving the foot runs between them. Thus they have cloven hoofs. The premolars and molars are usually different. The stomach is often complex and the cæcum is relatively small. The pigs and hippopotamuses, forming the group *Suina*, are the least specialised of these animals. In correspondence with their habit of dwelling in marshes and forests, where the ground is soft and a broad tread is needed, there are four well-developed digits on each foot, though the middle two alone touch the ground, and the

metacarpal and metatarsal bones are not fused into "cannon bones." The dental formula of the pig is $\frac{3, 1, 4, 3}{3, 1, 4, 3}$. The canines are large, grow throughout life like the incisors of the rabbit, and in the male form tusks; the grinding teeth are knobbed, not ridged, and the stomach has not the complicated form of that of animals that chew the cud. Cattle, with deer, giraffes, antelopes, and sheep, form the group *Ruminantia*. Here only the third and fourth digits are complete, and the fused metacarpals and metatarsals of these digits form "cannon bones."¹ The fibula is represented only by a small nodule of bone attached to the distal end of the tibia. There are no incisors or canines in the upper jaw, the dental formula being $\frac{0, 0, 3, 3}{3, 1, 3, 3}$. The ridges of the grinding teeth are crescentic and run fore and aft along the jaw. Such teeth are called *selenodont*. The animals "chew the cud," and

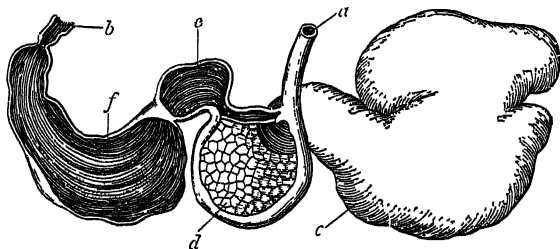


FIG. 258.—The stomach of a sheep.—From Leunis.

a., Esophagus; *c.*, rumen or paunch; *d.*, reticulum or honeycomb-bag; *e.*, psalterium or manyplies; *f.*, abomasum or reed; *b.*, beginning of duodenum

in connection with this habit have a complicated stomach, with four compartments, shown in Fig. 258. The food when it is first swallowed passes into the *rumen* or *paunch* at the left-hand end of the organ, the walls of which are beset with small processes or villi. Here it is kept till the animal is ready to chew it, becoming meanwhile somewhat softened. It is then passed back into the mouth, chewed up, and mixed with saliva. When it is swallowed again it passes along a muscular groove on the upper side of the second division of the stomach, known as the *reticulum* or *honeycomb-bag* from the pattern on its mucous membrane, into the *psalterium* or *manyplies*. The folded walls of this chamber, covered with papillae, serve as a filter, through which the food passes to the *abomasum* or *reed*, where the gastric juice is secreted. Paired outgrowths of the frontal bones are common in ruminants. In the cattle, antelopes, sheep, and goats they are permanent and capped with hardened epidermis, the structures thus formed

¹ Vestiges of the second and fifth digits are found in deer.

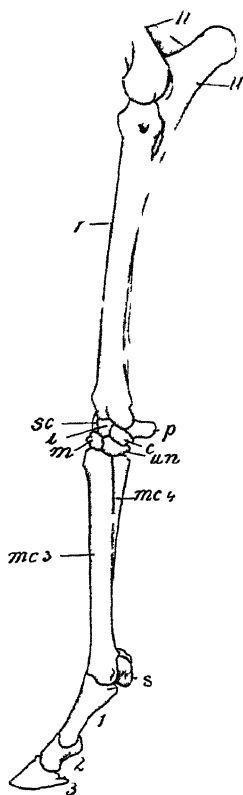


FIG 259 — A side view of the lower part of a pony's foreleg — From Thomson

h Distal end of humerus *u* olecranon process of ulna *r* radius, *sc*, scaphoid *l* lunate *c* cuneiform *m* os magnum *un*, unciform *p*, pisiform *mc 4*, splint of fourth metacarpal *mc 3*, third metacarpal, *s*, sesamoid 1 2 3 phalanges of third digit

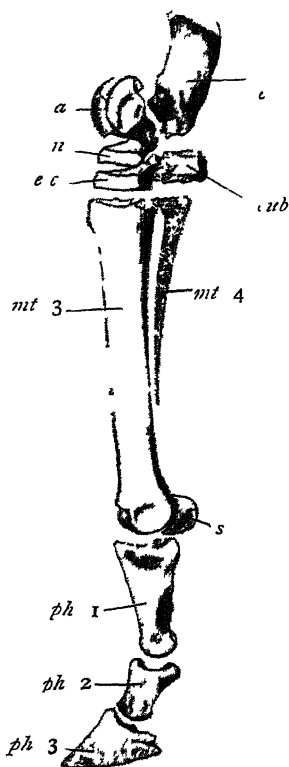


FIG 260 — A side view of the ankle and foot of a horse — From Thomson

a Astragalus, *c* calcaneus *n*, navicular *ec*, external cuneiform, *cub*, cuboid, *mt 3*, third metatarsal *mt 4* splint of fourth metatarsal *s*, sesamoid, *ph 1-3*, phalanges of third digit

being known as *horns*. In deer they lose their skin and form purely bony *antlers*, which are shed yearly.

In the *Perissodactyla* the middle or third digit of each foot is larger than the others and symmetrical in itself. In horses it is the only complete digit. The premolars and molars are alike and have broad, transversely ridged crowns. The stomach is simple, the cæcum is large, and there is no gall bladder. Horses, asses, and zebras belong to the genus *Equus*. Here there is in each foot only one functional digit—the third—with splints representing the metacarpals and metatarsals of the second and fourth. The wrist of the horse is known as the “knee,” the ankle as the “hock.” The metatarsals and metacarpals are the “cannon bones,” and the three phalanges of the single toe are the “pastern,” “coronet” or “little pastern,” and “coffin bone”

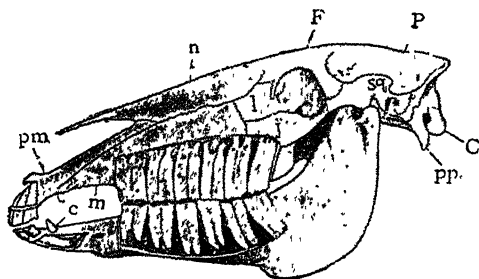


FIG. 261.—A side view of a horse's skull, roots of teeth exposed.
—From Thomson.

P., Parietal, F, frontal; n, nasal, pm, premaxilla; m, maxilla; j, jugal; l, lachrymal; sq, squamosal; pp, paroccipital process, c, canine or “tush”; C, condyle

respectively. The latter bears the hoof. The dental formula of the horse is $\frac{3, \frac{1}{2}, 3, 3}{3, 1, 3, 3}$. The ridges on the grinding teeth are complicated, some running along and some across the tooth. The enamel on the tips of the incisors is folded in, so as to form a pit. This gives rise to a marking which alters as the teeth wear down, and enables the age of the animal to be told.

The *Proboscidea* or Elephants are generally classed with the ungulates. They have all five toes. The trunk is a muscular extension of the nose, with the nostrils at the end. The tusks are the two upper incisors and are composed of solid dentine or ivory. There are no canines, but the six grinding teeth are very large and

transversely ridged, and are developed one at a time, so that there is a succession of them, each being replaced as it

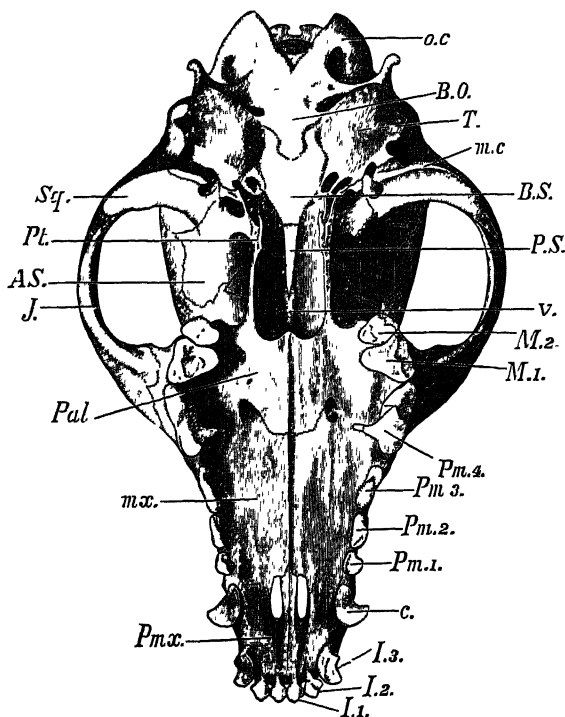


FIG. 262.—The lower surface of a dog's skull.—From Thomson.

o.c., Occipital condyle; *B.O.*, basioccipital; *T.*, tympanic bulla; *m.c.*, postglenoid process behind fossa for condyle of mandible, *B.S.*, basisphenoid; *P.S.*, base of presphenoid; *V.*, vomer, *M.2.*, second molar; *M.1.*, first molar; *Pm 1-4.*, premolars, the 4th the large carnassial; *c.*, canine; *I.1-3.*, incisors; *Pmx*, premaxilla, *mx*, maxilla; *Pal*, palatine; *J.*, jugal; *A.S.*, alisphenoid; *Pt*, pterygoid, *Sq*, squamosal (the reference line points to the glenoid fossa).

wears out. The testes do not descend into scrotal sacs. The *Hyracoidea*, usually placed near the Elephants, are little rabbit-like animals found in Palestine and Africa. *Hyrax*, the "coney" of Scripture, is the best known example.

Among the other groups of Eutheria are : the *Rodentia*, to which belong rabbits, rats, mice, squirrels, etc., all characterised by two pairs of large incisors adapted for gnawing and by the absence of canines ; the *Insectivora*, to which belong moles, hedgehogs, and shrews, with sharp-cusped teeth and a long snout ; the *Chiroptera* or bats, in which the fore-limb becomes a wing by the lengthening of its digits and the formation of a web of skin between them and the side of the body ; and the *Carnivora*, to which belong dogs, cats, bears, and seals. These latter are generally bold, intelligent animals. They have claws, which in the cats are retractile. The canines are strong and sharp, and some of the back teeth are adapted by their narrow, blade-like crowns for cutting flesh. These are the fourth upper premolar and the first lower molar. The dental formula of the dog is $\frac{3, 1, 4, 2}{3, 1, 4, 3}$.

Dogs and cats are digitigrade and, like most of the other forms, have five fingers and four toes. The clavicles are rudimentary.

The last group of mammals which we shall mention is the *Primates*, which include monkeys and man, together with the lemurs, which link the monkeys to other mammals. The Primates are plantigrade, and either their thumb or their great toe—usually both—can be opposed to the other digits so as to grasp objects. There are well-developed clavicles, and the upper arm and thigh are free, as in the elephants, not enclosed in the skin of the trunk, as in most mammals. The orbits are enclosed behind by a complete bony wall and are turned forwards, not, as is usual, to the sides. The majority of these peculiarities are connected with an arboreal habit. It should be noted that in most respects the Primates, and man with them, are not highly specialised animals. In their limbs, in their teeth, in the possession of clavicles, and in the alimentary canal they present a type of organisation which is on the whole below, rather than above, the average of specialisation in the Mammalia.

Man is related to a group of tailless, half-erect monkeys which includes the gibbons, chimpanzee, gorilla, and orang-utan. From these he differs far more strikingly by his mental attributes than by his physical features, but the following points are of

interest. Man alone walks perfectly upright. His legs are longer than those of the great apes, and the great toe is not opposable. He is less hairy. He has a better command over his voice. His brain is twice the size of that of the gorilla, which in this respect approaches him most nearly, and its convolutions are more complex than those of the great apes. The cranial part of his skull is correspondingly enlarged. When the face is forwards the foramen magnum looks downwards, instead of more or less backwards, as in most other mammals. The dental formula is $\begin{smallmatrix} 2, 1, 2, 3 \\ 2, 1, 2, 3 \end{smallmatrix}$, which is that of the great apes, but the small size of the canines and the absence of a gap between them and the incisors are peculiar to man. The chin and the projection of the nasal bones to support the nose are also human features.

CHAPTER XXII

EMBRYOLOGY

HITHERTO we have been concerned almost wholly with the anatomy and physiology of adult animals. We must now give some attention to the process by which the adult arises from the fertilised egg. For this purpose we shall study first the development of the lancelet, which is relatively simple and easy to follow owing to the fact that the protoplasm of the ovum is not hampered with a large amount of yolk. The egg is about .1 mm. in diameter, covered with a slight vitelline membrane. The first cleavage is vertical and forms two equal blastomeres (p. 107). The second is also vertical, at right angles to the first, the third nearly equatorial, dividing each blastomere into a rather smaller upper half and a rather larger lower half. The blastomeres do not meet in the middle, so that at this stage they form a ring. By repeated divisions, vertical and horizontal, a hollow sphere or *blastula* arises, whose cavity or *blastocœle* is walled by a single layer of cells, rather larger and with more yolk granules on one side. This side becomes first flattened and then tucked or *invaginated* into the blastocœle, till the latter is practically lost and a two-layered cup or *gastrula* has arisen. In spite of the difference in shape we may compare this with the body of a *Hydra*. The outer layer of the body is the ectoderm or *epiblast*, and the inner layer the endoderm or *hypoblast*, the hollow of the cup is the primitive gut or *archenteron*, and the mouth, as yet wide, is called the *blastopore*. The gastrula now lengthens, owing to the growth of the blastopore lip. This growth is at first more rapid on the side which corresponds to the future dorsal side of the body, but afterwards the ventral side grows the

more rapidly. As a result the blastopore becomes a small opening at what will be the hinder end of the body.¹ One (the dorsal) side becomes flattened, and the blastopore comes to lie at the extreme hinder end of this. Meanwhile the cells of the epiblast develop cilia, by means of which the gastrula revolves within the vitelline membrane, and the cells of the flat dorsal side become more columnar and form a distinct strip known as the *neural or*

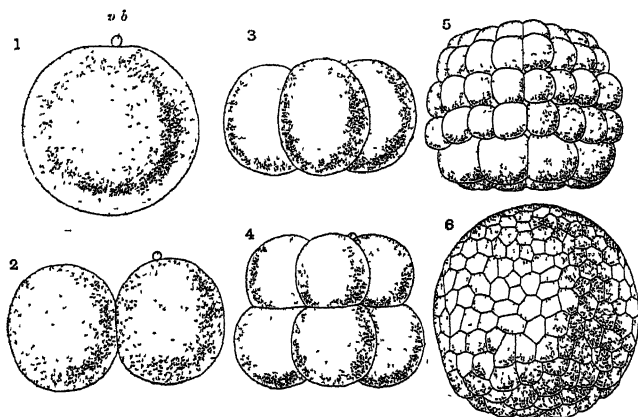


FIG. 263.—Stages in the cleavage of the ovum of *Amphioxus*.—After Hatschek.

1, Unfertilised egg; 2, stage of two blastomeres; 3, stage of four blastomeres; 4, stage of eight blastomeres; 5, stage of seventy-two blastomeres; 6, blastula, *p.b.*, polar body.

medullary plate. The epiblast at the sides of this plate now becomes detached from it and grows over it, enclosing a small space. This process begins at the hinder end, so that the blastopore is covered and opens into the space in question. The sides of the neural plate then fold upwards and meet above the space, so as to form a tube which will become the nerve cord. Its hollow is the *neural canal*, and the blastopore, which is now known as the *neurenteric*

¹ The details of the narrowing of the blastopore are a matter of dispute.

canal, leads from it to the gut. Eventually the neurenteric canal closes. An opening, known as the *neuropore*, long remains at the front end of the neural canal and puts it into communication with the olfactory pit (p. 273). Meanwhile the hypoblast under the neural plate has also been undergoing a folding, by which it gives rise to the notochord

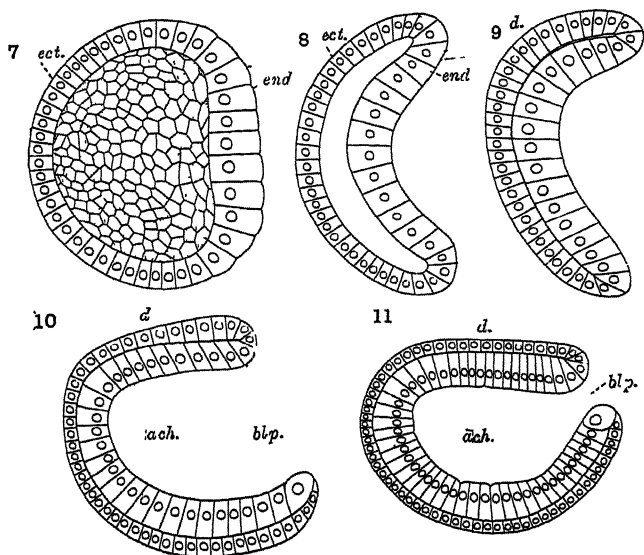


FIG. 264.—Stages in the gastrulation of *Amphioxus*. Modified.—After Hatschek. In 7 a half blastula is shown; 8–11 are sections.

ach., Archenteron; *bl.p.*, blastopore; *d.*, future dorsal side; *ect.*, ectoderm; *end.*, endoderm. The position is not the same as in Fig. 263, the large cells being to the right instead of below.

and to the mesoderm, which at this stage is known as *mesoblast*. The notochord is formed by a median longitudinal groove which becomes constricted off from the gut from before backwards, its cells eventually rearranging themselves to form a rod and becoming vacuolated. Its front end grows forwards to the end of the snout. The hind end is for a long time connected with the hypoblast in

front of the neurenteric canal. The mesoderm arises as five hollow outgrowths. One of these is median and unpaired in front. Behind it lies a pair of dorso-lateral pouches at the sides of the notochord, and behind these two long dorso-lateral grooves. The median and first two lateral pouches soon separate from the gut, though the left one retains a narrow connection for some time, but the grooves, as fast as they close off in front, are prolonged backwards. As growth progresses the separated anterior part of the groove becomes segmented into a series of pouches like the first pair. These pouches are the *mesoblastic*

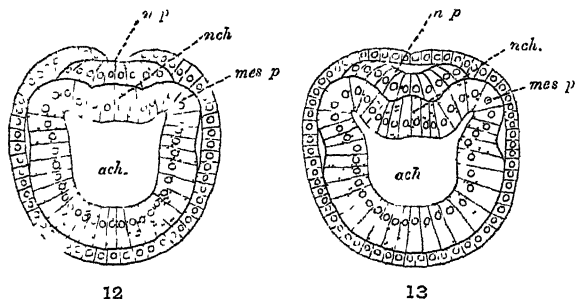


FIG. 265 — Transverse sections of embryos of *Amphioxus* at two stages somewhat later than that represented by 11 (Fig. 264), showing the origin of the nerve cord, notochord, and mesoblast. — After Hatschek
ach., Archenteron; *mes p.*, pouch which will become first mesoblastic somite; *n p.*, neural plate; *nch.*, rudiment of notochord.

somites. The rudiments of all three layers of a triploblastic animal are now present. Epiblast, hypoblast, and mesoblast are known as the *germ layers*, and though, as we shall see, they arise in different ways in different cases, they are present at an early stage in the embryos of all triploblastica. Before these processes are complete *hatching* takes place by the throwing off of the vitelline membrane, and the embryo becomes a larva. Until the formation of the mouth the animal is sometimes called the "free embryo."

Hatching takes place about eight hours after fertilisation. About twenty-four hours later the mouth is formed as a small opening, which rapidly enlarges, on the left side

of the forepart of the body. At the same time, by perforation from within outwards, the first gill-slit is

Larva.

formed as a median ventral opening which shifts upwards to the right side of the body. As we shall see, this slit belongs to the *left* side of the body of the adult. The anus is formed shortly after the first gill-slit, much nearer the hind end of the body than it is in the adult. Development henceforward takes place more slowly, the animal becoming adult in about three months. We will consider first the external features of its metamorphosis. More gill-slits are formed in the mid-ventral line, and each in turn shifts on to the right side. They are primary slits, and each except the first acquires a tongue-bar.

When fourteen of these slits have been formed, another series appears above them on the right-hand side. There are eight in number. Six of the first series

of slits disappear, so that the number in the two series is the same. While the formation of the second series of slits is taking place both series shift downwards, the original series passing over to the left side of the body, while the second series remains on the right. At the same time the mouth also shifts to its adult position in the middle line. The slits at first open directly upon the surface of the body, but at an early stage, when there are as yet only six clefts of the first series, two ridges appear, one on each side of the slits. In correspondence with the position of the slits these

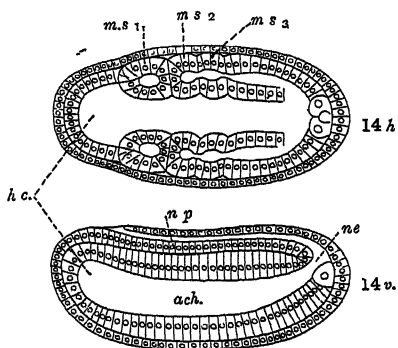


FIG. 266 — Vertical (14v) and horizontal (14h.) longitudinal sections of an embryo of *Amphioxus* at a somewhat later stage than that represented by 13 (Fig 265).— After Hatschek.

ach., Archenteron; *h.c.*, region which will become the anterior median pouch, or head cavity, *m.s. 1-3*, mesoblastic somites; *n.p.*, neural plate, *n.e.*, neurenteric canal

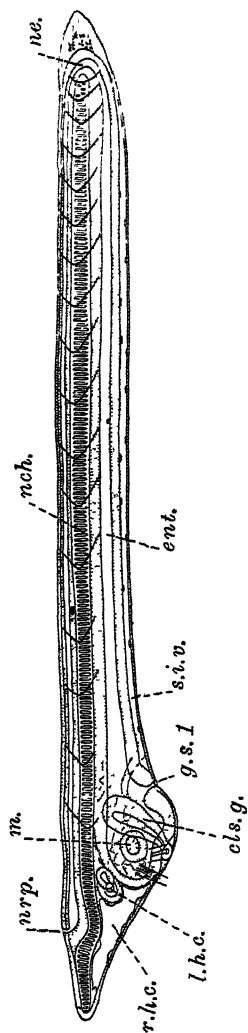


FIG. 267.—A larva of *Amphioxus* at the stage at which the first gill-slit has been established.—After Hatschek.
cls.g., Club-shaped gland, *ent.*, gut, *g.s.l.*, first gill-slit, *l.h.c.*, left head cavity, now opening to the exterior; *m.*, mouth, *m.p.*, notochord; *n.p.*, neurenteric canal; *nch.*, neuropore, *r.h.c.*, right head cavity, *s.i.v.*, subintestinal vein

ridges lie in front on the right side of the body, but behind curve down to the ventral side, where the new slits are forming. These ridges are the metapleural folds. From the inner face of each a secondary ridge grows inwards to meet its fellow and enclose a space below the body. This is the rudiment of the atrium. As the ridges do not meet behind, there is left an opening which becomes the atriopore. The closure of the atrium takes place from behind forwards as the folds shift downwards with the clefts, from the right side of the body to their permanent position. The atrium is at first small, but enlarges so as to enclose the sides of the body. The endostyle appears at the beginning of the larval period as a band of columnar ciliated cells on the right side of the anterior end of the pharynx above the first gill-cleft. It becomes folded as a V with the apex directed backward. When the two rows of clefts are established, the apex of this V grows back between them, the two limbs fusing to form a single strip. As the clefts move downwards the endo-

style between them moves also. A structure known as the *club-shaped gland* is formed from the wall of the pharynx on the right side above the gill-clefts. It disappears while the second series of clefts is forming.

We must now consider the fate of the mesoblastic somites. The anterior median outgrowth divides into right and left halves, of which the right becomes a cavity in the snout of the adult, while the left opens to the exterior and becomes a small pit in the wheel organ. Each of the somites of the first pair sends forward into the snout an outgrowth, which gives rise to a cavity in the head of the adult, while its walls form part of

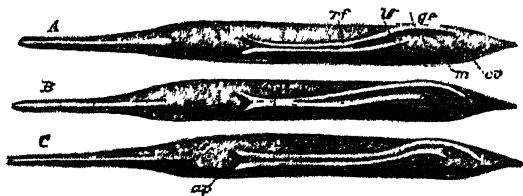


FIG. 268.—Three larval stages of *Amphioxus*.—After Lankester and Willey.

In *A* the metapleural folds are still separate; in *B* they are united behind; in *C* they are united along their whole length.

ap, Atriopore; *co*, ciliated pit derived from the left anterior coelomic division of the coelom; *g.e.*, gill-slits; *l.f.*, left metapleural fold; *m.*, mouth; *r.f.*, right metapleural fold.

the mesoderm of the same region. The rest of the somite gives rise to other spaces in the neighbourhood of the mouth and by backward outgrowths to spaces in the metapleural folds. In the adult these latter spaces are represented by lymph canals of doubtful origin. The walls of the spaces give rise to mesodermal tissues around the mouth and in the metapleural folds and to the first myomere. The remaining mesoblastic somites all behave alike. They extend downwards on each side till they meet below the gut. The outer or *somatic* wall of each lies against the epiblast, together with which it is known as the *somatopleure*; the inner or *splanchnic* wall lies against the hypoblast and is known with it as the *splanchnopleure*. The longitudinal

septum or ventral mesentery between the cavities of the two sides now breaks down, so that they become continuous. At the same time there forms in each of them a horizontal septum which divides it into a dorsal half and a ventral half. The cavity of the ventral portion is known as the *splanchnocœle*. The septa between the splanchnocœles break down so that they form a continuous

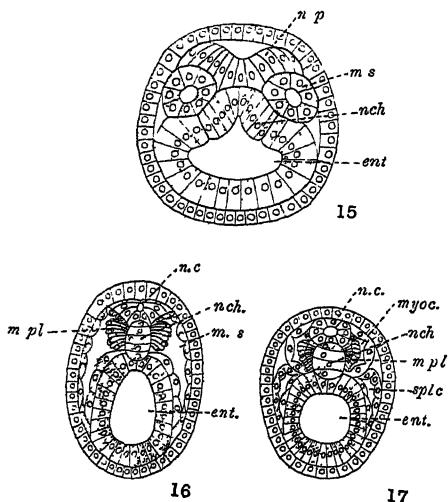


FIG. 269.—Transverse sections of embryos of *Amphioxus* at successive stages later than that represented by 14 (Fig. 266).—After Hatschek.

ent., Gut or enteron; m.pl., muscle plate; m.s., mesoblastic somite; myoc., myocœle; n.c., nerve cord; n.p., neural plate; n.ch., notochord; spl.c., splanchnocœle.

perivisceral cavity, which afterwards becomes broken up in the pharyngeal region into a series of tubes by the appearance of the gill-clefts (p. 269). The cavities of the dorsal parts of the somites remain separate and are known as *myocœles*. Their inner walls, against the notochord, become greatly thickened to form each a structure, known as a *muscle plate*, which gives rise to a myomere, the walls between successive myocœles giving rise to connective

tissue septa between the myomeres, and the outer walls of the myocœles to the dermis. From the inner wall of each dorsal division of a somite, below the muscle plate, an outgrowth burrows its way between the muscle plate and the notochord and forms from its wall the connective tissue sheath of the notochord and nerve cord. This outgrowth is known as the *sclerotome*, the part which forms the muscles being known as the *myotome*. Lastly, a downgrowth from each dorsal division in the pharyngeal region gives rise to a gonad.

During the external and internal changes which we have traced, the larval *Amphioxus* swims freely in the sea, usually at a depth of a few fathoms from the surface. As its metamorphosis reaches completion, it sinks to

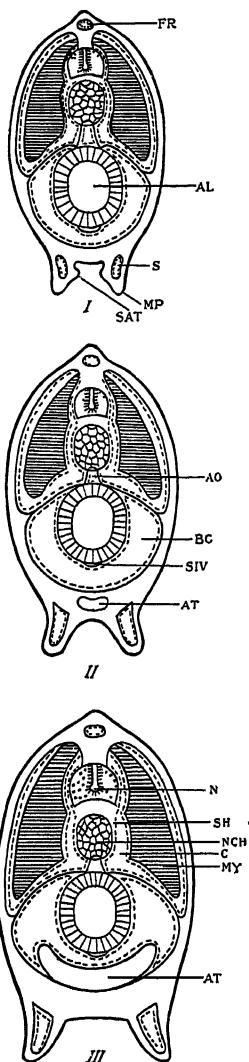


FIG. 270.—The development of the atrial chamber in *Amphioxus*. — After Lankester and Willey.

In I the metapleural folds are seen sending a slight projection inwards. In II the two projections have united and enclose a small space (AT), which is the rudiment of the atrial chamber. In III. this space is enlarging at the expense of the coelom. A comparison of this figure with the cross-section of the adult (Fig. 182) will show the relation of coelom and atrial chamber.

FR., Cœlomic space within dorsal fin, AL, gut; S., cœlomic space of metapleural fold; MP, metapleural fold, SAT., projection which forms floor of atrial chamber; AO., aorta; B.C, cœlom; S.I.V., sub-intestinal vein; N, nerve cord; SH., sheath of notochord; MY., myotome; C., cavity of sclerotome; AT., atrial chamber. The dotted line indicates the mesodermic wall of the coelom.

the bottom and takes up the burrowing habits of the adult.

The ovum of the frog has been described on p. 90.

The first division of its cleavage separates two similar cells, each containing, like the ovum, an upper, black, pigmented portion and a lower, white, yolky portion. The second division is at right angles to the first and forms four similar blastomeres; the third division is horizontal and separates four small, pigmented upper blastomeres from four large, yolky lower blastomeres. By succeeding divisions sixteen and then thirty-two blastomeres arise, after which cleavage becomes irregular, the pigmented cells dividing more rapidly than the yolky. The final result is the formation of a blastula, in which the floor of the blastocœle is composed of large yolky cells and the roof of small pigmented cells. At the sides the upper cells merge

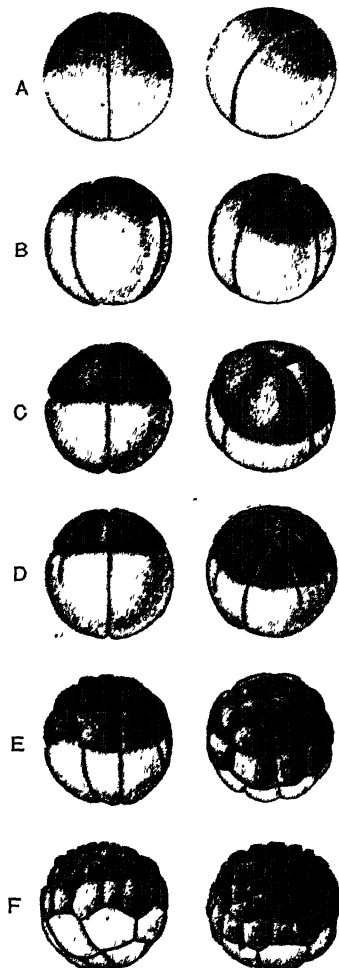


FIG. 271.—Stages in the cleavage of the frog's egg. Of each stage two views are given, one showing it from the side, the other obliquely from above. A-F show successively stages with two, four, eight, sixteen, thirty-two, and numerous blastomeres.

gradually into the lower. The pigmented cells are the future epiblast, the yolk cells will give rise to the hypoblast, and both regions differ from the corresponding parts of the blastula of *Amphioxus* in being more than one cell deep, though the white layer is much thicker than the black. From this blastula a gastrula is formed, not by invagination, which would be impossible on account of the relative amount of the two layers, but by an overgrowing of the epiblast over the yolk cells.

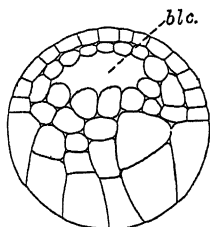


FIG. 272.—A vertical section of a frog's egg at the end of cleavage.

blc., Blastocœle

When this process begins, the black epiblast and the white yolk cells each form half the outer surface of the blastula, which floats with the black side uppermost. The epiblast grows downwards over the surface of the yolk cells, narrowing the exposed area of the latter. This extension of the epiblast is due to the division of the cells at the circumference of the white area in such a way as to separate small epiblast cells outside from large hypoblast cells inside, the epiblast cells becoming pigmented as they form. Thus a skin of epiblast is, as it were, cut off from the surface of the yolk cells. This process is known as *epiboly*. If it took place

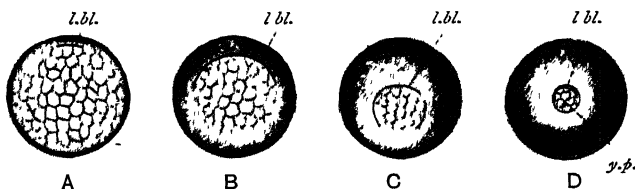


FIG. 273.—Stages in the gastrulation of the frog's egg. The egg is seen from the lower, white pole, which faces towards the future hind end of the animal.

l.bl., Lip of the blastopore; *y.p.*, yolk plug.

all over the surface of the yolk cells the result would be the formation of a close skin of epiblast over a solid mass of hypoblast without an enteron. But on one side of the white surface, just below the edge of the epiblast, there appears a small, shallow, crescentic slit, with its convex edge towards the black area. Where the advancing epiblast reaches this, the process by which it is extending changes

and is converted into a multiplication of the cells of the convex side of the slit, so that a fold or lip grows and projects over the yolk cells on the other side of the slit and a narrow space is enclosed between the arched lip and the yolk cells. This space is the enteron. The cells on the outer side of the lip are of course epiblast, continuous

with the rest of that layer. The cells of the inner side or lining of the lip are small hypoblast cells and form the roof of the enteron, its floor being formed by the large yolk cells over which the lip is growing. The lip is the upper edge of the blastopore, the rest of whose edge is as yet indefinite and represented by the limit of the advancing epiblast all round the egg. All this time the shape of the crescent is changing by its two ends lengthening and curving towards one another till at last they meet to form a circle. By that time the edge of the epiblast has reached this circle all round its circumference, so that all the yolk is covered except that within a circular area, the definitive blastopore, bordered by a continuous lip and filled by a *yolk plug* consisting of yolk cells which have not yet been covered. The lip continues to grow over the yolk plug, thus narrowing the blastopore. Finally, the plug is entirely covered and the blastopore is a minute opening at the bottom of a slight depression.

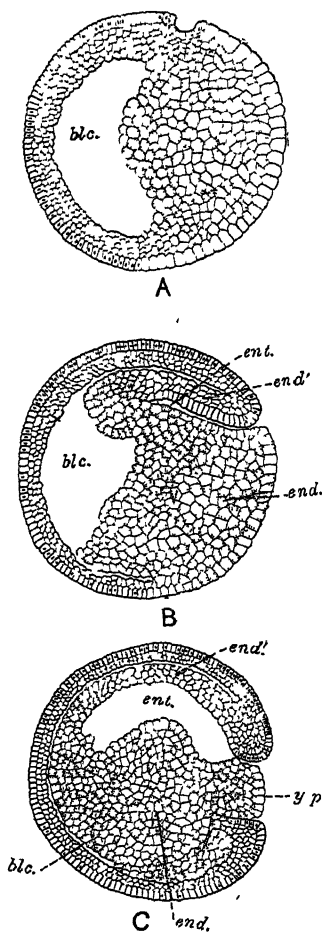


FIG. 274.—Sections of a frog's egg in successive stages of gastrulation. The sections are vertical and pass along the future longitudinal axis of the body, the hind end being to the right of the figure.

A, B, and C correspond roughly to A, B, and D of Fig. 273.

blc., Blastocœle; *end.*, yolky endoderm cells, *end'*, small endoderm cells, *ent.*, gut; *y.p.*, yolk plug in blastopore.

During the later stages of this process an internal movement of the yolk cells has obliterated the blastocoele and enlarged the enteron, which was at first a mere slit, so that it becomes a spacious cavity, which communicates with the exterior by a slit between the dorsal side of the blastopore lip and the yolk plug.

At the end of gastrulation the enteron is a large cavity with a very thick ventral wall composed of large yolk cells, many deep, and a thinner dorsal wall composed of smaller and fewer cells.

Formation of Mesoblast.

From this wall the mesoderm and notochord have already begun to form (Fig. 276). The former arises by the splitting off of an outer layer of cells which starts on the dorsal surface on each side of the middle line, in the same position in which the pouches arise in *Amphioxus*, and spreads outwards around the thick ventral wall of the gut. For a time the embryonic mesoderm or *mesoblast* remains connected with the hypoblast along the mid-dorsal line, but presently it separates here also, leaving in the middle a cord of cells attached to the dorsal wall of the gut. This soon separates as the notochord. The mesoblast

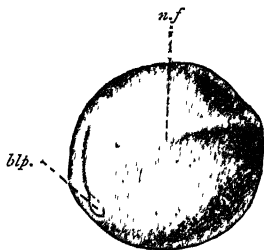


FIG. 275.—The embryo of a frog shortly after the completion of gastrulation, seen from the right side and somewhat from behind.

blp., Blastopore; *n.f.*, neural folds.

forms a sheet on each side of the gut, below which the two sheets soon meet, enclosing it completely except in the mid-dorsal line. On each side of this line the mesoblast is thicker than elsewhere, forming the *segmental plate*. A split, the rudiment of the coelom, appears and separates an outer or somatic layer from an inner or splanchnic layer. This split does not extend far into the segmental plate, from which it soon disappears. The segmental plates now divide into a series of blocks or mesoblastic somites, separating from the *lateral plates*, which do not segment. The somites form from before backwards, but the head region is not segmented in the frog, though it is so in the dogfish.

Meanwhile external changes have been taking place. The embryo at the end of gastrulation was still roughly spherical, the blastopore marking the future hind end. In front of this the future dorsal surface flattens to form the neural plate. The edges of this thicken to form the *neural folds*, which are continuous in front, and behind enclose the blastopore. On either side of the anterior end of the neural folds appears a thickening which becomes divided by a furrow into a *gill plate* and a *sense plate*. The neural

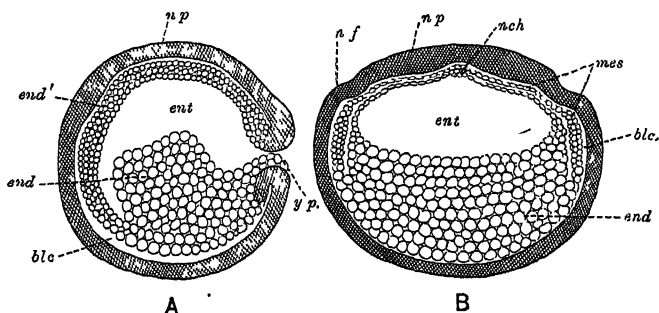


FIG. 276.—Sections of an embryo at about the stage of Fig. 275.

A, Vertical longitudinal; B, transverse

b.l.c., Blastocoele; end, yolky cells of endoderm; end', small cells of endoderm; ent, gut; mes, mesoderm; n.f., neural fold; n.p., neural plate; n.ch., notochord, y.p., yolk plug.

folds become closer, rise up, bend over, and meet so as to enclose the neural canal, their union taking place first about the middle of their length (Figs. 277, 278, 282, A). Since they enclose the blastopore, the latter comes to lead from the gut to the neural canal and gives rise to a neurenteric canal, but this soon disappears. The neural canal separates from the epiblast above it, formed by the outer walls of the neural folds, whose inner sides become the wall of the neural canal. Before the folds have united in front, the open canal between them is enlarged and then divided into three swellings, the rudiments of the fore-, mid-, and hind-brains. It will be seen

that in the frog, as in the lancelet, the central nervous system arises by the sinking in and folding off of a strip of the epidermis of the back. This process is found in all Chordata, and is of the highest importance in the drawing of comparison between them and other animals. During the formation of the central nervous system the body has been elongating and other structures appearing. Below the blastopore, in the area which it occupied before its contraction, there appears a pit known as the *proctodæum*, and an opening piercing through from this to the gut forms the anus. Above it a knob grows out to form the tadpole's tail. Grooves appear on each gill plate marking out the visceral arches, and upon the first two branchial arches branched *external gills* grow out. Below the head a median pit of epiblast forms the *stomodæum*, which will eventually break through to the enteron and become the mouth. Behind the stomodæum is a horseshoe-shaped sucker; above it a pit in each of the sense plates gives rise to the olfactory organ. When these changes are complete the animal hatches. This happens about a fortnight after the eggs are laid.

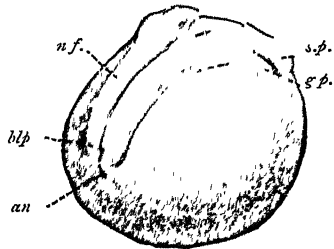


FIG. 277.—An embryo of the frog at a later stage.

an, Proctodæum (invagination which will form anus), *blp.*, blastopore; *g.p.*, gill plate, *n.f.*, neural fold; *s.p.*, sense plate.

In the external development of the tadpole (Fig. 6) the following changes take place. A third pair of external gills is formed, and the mouth opens and is provided with a pair of horny jaws, which are eventually lost. Meanwhile four gill-clefts open, and the external gills wither, being replaced by new gills on the walls of the clefts. The latter represent the first to fourth branchial clefts of the dogfish, the external gills standing on the first three branchial arches. Shortly after the appearance of the clefts a fold of skin grows back from each side of the head so as to cover them. The folds

**External
Features
of Larva.**

are the *opercula*, they meet ventrally, and presently their hinder edges fuse with the body everywhere, except in one spot on the left side, where an opening is left for the discharge of the water used in breathing. The sucker now begins to degenerate. Shortly afterwards rudiments of the hind-limbs appear at the base of the tail, as a pair of small knobs, which increase rapidly and become first

jointed and then divided into toes. The fore-limbs arise at the same time as the hind limbs, but as they are covered by the opercula

B they are not seen till a later stage. About the end of the second month the lungs which have been forming come into use and the gills begin to degenerate, and a fortnight later the tadpole begins to turn into a young frog. The outer layer of the skin and the horny jaws are thrown off, the mouth enlarges and changes its shape, the fore-limbs appear, that on the left being pushed through the gill opening, that on the right breaking through the operculum, the gill-clefts close, and finally the tail shortens and is ab-

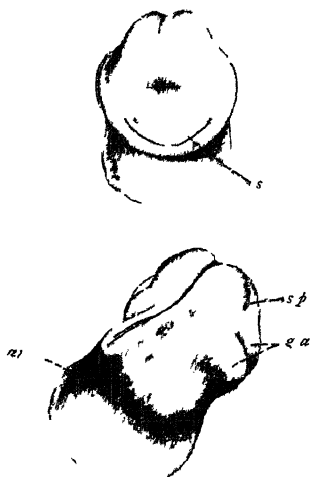


FIG 278 —A still later embryo

A From behind and above B, from in front

an, Proctodæum, ga, gill arches, s, sucker sp, sense plate

sorbed, and the metamorphosis is complete

We have traced the internal development of the embryo up to the establishment of the three layers of

Germ Layers

the body of a triploblastic animal. Only an outline of the further development of these layers can be given. From the epiblast or embryonic ectoderm arise the epidermis, nervous system, sense organs, and lining of the mouth and cloacal opening, from the hypoblast or embryonic endoderm arises the lining of the greater part

of the gut, the lungs, liver, pancreas, and thyroid, and the notochord; from the mesoblast or embryonic mesoderm arise the skeleton, connective tissues, muscles, vascular

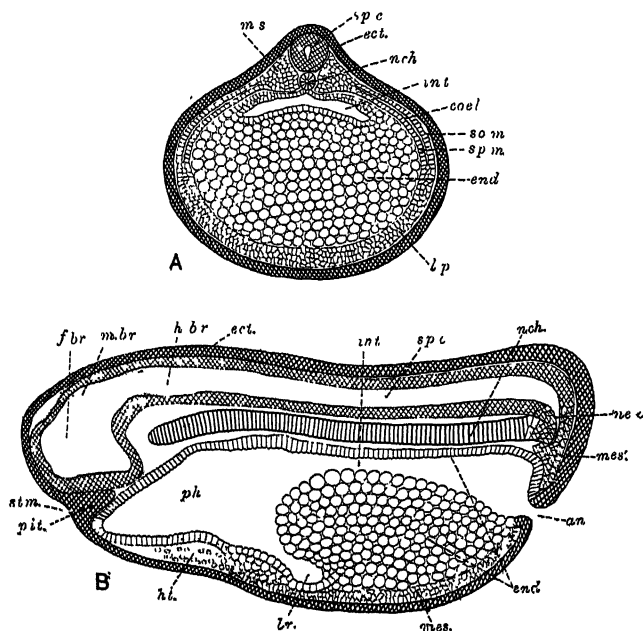


FIG. 279.—Sections of an embryo frog at about the stage of Fig. 278.

A, Transverse; B, longitudinal.

an., Anus; *coel.*, coelom; *ect.*, ectoderm or epiblast; *end.*, endoderm or hypoblast; *f.br.*, fore-brain; *h.br.*, hind-brain; *ht.*, rudiment of heart; *int.*, intestine; *l.p.*, lateral plate of mesoblast; *lr.*, rudiment of liver; *m.br.*, mid-brain; *ms.*, mesoblastic somite; *mes.*, mesoblast; *mes'.*, mesoblast continuous with epiblast of neural canal and hypoblast of notochord; *ne c.*, neurenteric canal; *nch*, notochord; *ph.*, pharynx; *pit*, rudiment of pituitary body; *so.m.*, somatic mesoblast; *sp.c.*, spinal cord; *sp.m.*, splanchnic mesoblast; *stm.*, stomodæum.

system, excretory organs, and generative organs. The skeletal tissues and unstriped muscle arise from a loose kind of mesoderm, known as *mesenchyme*, formed of cells budded off by the compact mass around the coelom and perhaps also by the ectoderm and endoderm. The mass

around the coelom is known as *mesothelium*, and from it arise all the remaining mesodermal tissues.

The origin of the central nervous system has already been described. The dorsal roots of the nerves are formed as outgrowths of the edges of the neural plate before the neural folds have met. The ventral roots arise later, as outgrowths from the side of the central nervous system, and in the spinal cord become connected with the dorsal roots. The formation of the olfactory organs has been mentioned. The posterior nares arise from the olfactory chambers as downgrowths which break through into the mouth. The labyrinth of the

**Nervous
System and
Sense Organs.**



FIG 280.—A frog embryo at the stage of hatching.

an., Proctodæum; *an.c.*, slight swelling over the rudiment of the ear; *e.g.*, external gills on gill arches; *na*, invagination to form nasal capsule, *o.c.*, slight swelling over the rudiment of the eye; *s.*, sucker; *stm*, stomodæum (invagination which will form the mouth).

ear is formed from the deeper layer of the epiblast as an ingrowth which forms a vesicle, but does not open to the exterior. It gradually takes on the shape of the labyrinth by the formation of septa which grow into it and divide it up. The eye has a more complicated origin. The retina and the pigmented epithelium arise from a pair of outgrowths of the fore-brain, known as *optic vesicles*, which grow out towards the sides of the head soon after the closure of the neural tube. Each takes on the form of a hollow bulb on a hollow stalk. The stalk gives rise to the optic nerve. The outer half of the bulb becomes thickened and then folded back into the inner half, as a hollow indiarubber ball may be folded if it be damaged. The two-layered cup which thus arises is known as the *optic cup*. The thick layer which lines it is

the retina, the thin layer on the side towards the stalk is the pigment layer. From the deeper layer of the epiblast there arises a thickening which projects into the mouth of the cup, separates from the epiblast, and becomes the lens, after passing through a stage in which it is a hollow vesicle.

The alimentary canal arises from three rudiments the epiblastic stomodæum of fore-gut, which forms the mouth, the hypoblastic mesenteron or mid gut, which forms the greater part of the canal, and the epiblastic proctodæum or hind-gut, which forms the cloacal opening. The pituitary body arises as an outgrowth from the roof of the mouth. The gill-slits are formed by outgrowths from the (hypoblastic) pharynx, which meet and perforate the skin. The first of them, corresponding to the spiracle of the dogfish, never opens, but forms the tympanic cavity and Eustachian tube. Between, in front, and behind the clefts mesoblastic thickenings constitute the visceral arches, in which skeletal and vascular structures corresponding to those of the dogfish arise. The liver, pancreas, and lungs arise as ventral outgrowths from the gut. The thyroid body starts as a median longitudinal groove in the floor of the pharynx. This gives rise to a solid mass of cells which separates from the pharynx and divides into two. The intestine of the tadpole, when the

Alimentary Canal

FIG 281.—A diagram of a transverse section of the frog embryo at the hatching stage

cal, Coelom *ect*, ectoderm *int* intestine *lr*, liver, *m pl*, muscle plate, *nch*, notochord, *nst*, nephrostome, *s d* segmental duct, *spc* spinal cord. The glomeruli are seen opposite the nephrostomes.

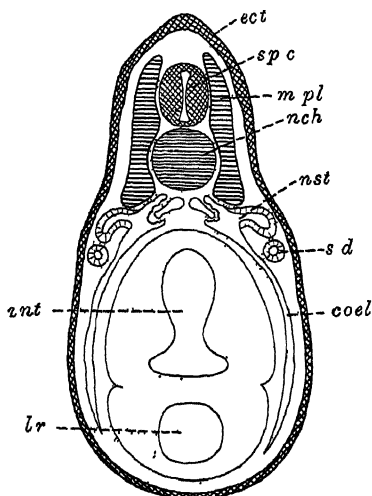


FIG 281.—A diagram of a transverse section of the frog embryo at the hatching stage

cal, Coelom; *ut*, ectoderm; *int*, intestine; *lr*, liver; *mpl*, muscle plate; *nch*, notochord; *nst*, nephrostome; *sd*, segmental duct; *spc*, spinal cord. The glomeruli are seen opposite the nephrostomes.

yolk in its ventral wall has been absorbed, becomes for a time more coiled than that of the adult frog, probably in correspondence with the vegetable diet.

We have seen that the body cavity or coelom is developed as a split in the mesoblast plates. The cells of

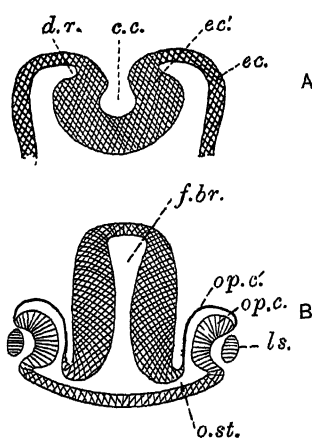


FIG. 282.—Diagrams to illustrate the formation of the central nervous system of the frog.

A, The folding off of the neural canal;
B, transverse section of the fore-brain at the hatching stage.

c c, Neural canal; d.r., position in which dorsal root arises, ec, epiblast; ec', infolding of the epiblast of the neural plate to form central nervous system; f.br., fore-brain, ls, lens; op.c., inner wall of optic cup, which will form retina proper; op.c., outer wall, which will form pigment layer; o.st., stalk of optic vesicle.

Mesoblastic Tissues.

the splanchnic and somatic layers which face towards this form the coelomic epithelium. The greater part of the coelom becomes the abdominal or peritoneal cavity, surrounding the gut on all sides except in the mid-dorsal line, where the mesentery is left. A forward ventral prolongation of the coelom becomes the pericardial cavity. The muscles of the gut arise from the splanchnic layer, the body muscles from the mesoblastic somites, which give rise to myotomes, though the regular arrangement of these is lost in the adult. The bulk of the skeleton is at first laid down in cartilage, which in places becomes converted into bone and in places is reinforced by membrane bones, as has been explained in the chapter on the skeleton of the adult. The first

rudiment of the cranium has the form of a pair of curved longitudinal bars, the *trabeculae*, lying below the brain, and joined behind to a pair of *parachordal plates* at the sides of the front end of the notochord, which projects into the floor of the tadpole's skull as it does into that of the dogfish. Between the trabeculae is at first a space or "fossa," in which

lies the pituitary body. These structures fuse with one another and with the cartilaginous nasal and auditory capsules, and upgrowths from them form the sides and eventually the roof of the cranium. The pituitary opening presently closes. The skeleton of the upper jaw is at first a continuous palato-ptyerygo-quadrata bar of cartilage forming a part of the cartilage of the mandibular arch. The hyoid apparatus of the adult is the remains of the skeleton of the hyoid and branchial arches of the tadpole.

The heart appears some time before hatching. It is at first a straight tube, which arises below the pharynx. Subsequently the tube is thrown

Blood Vessels.

into an S shape and becomes divided by partitions into the several chambers. The endothelium or pavement epithelium which lines the heart arises by the rearrangement of some scattered cells which lie between the splanchnic layer of mesoblast and the ventral hypoblast of the gut, and the muscular tissue is formed by a folding of the splanchnic layer itself. The space between the splanchnopleure and somatopleure in the region of the heart, which at this time is continuous with the rest of the coelom, forms the pericardial cavity. The

communication between the pericardial and abdominal cavities is abolished by the formation of the great veins. The venous system is at first arranged on the same plan as in the dogfish, with two ductus Cuvieri and anterior and posterior cardinal veins. Subsequently the posterior cardinal veins disappear and are replaced by the inferior vena cava, the ductus Cuvieri becoming the superior venæ cavæ. The arterial system of the tadpole closely resembles that of a fish. The conus arteriosus leads into a long ventral aorta, from the end of which arise four vessels to the branchial arches.¹ From

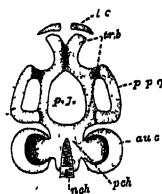


FIG. 283.—A diagram of the rudiment of the skull in a tadpole.

au c, Auditory capsule; *L.C.*, labial cartilage, *nch*, notochord; *P.P.Q.*, palato-ptyerygo-quadrata bar; *pch*, parachordal, *trab*, trabecula.

¹ There are traces of similar vessels in the hyoid and mandibular arches.

the gill capillaries there arises in each arch an efferent vessel which discharges into a longitudinal suprabranchial artery. The two suprabranchial arteries join behind to form the dorsal aorta. In front they are continued as the common carotids. In the presence of a single efferent vessel in each arch and the two suprabranchial arteries the

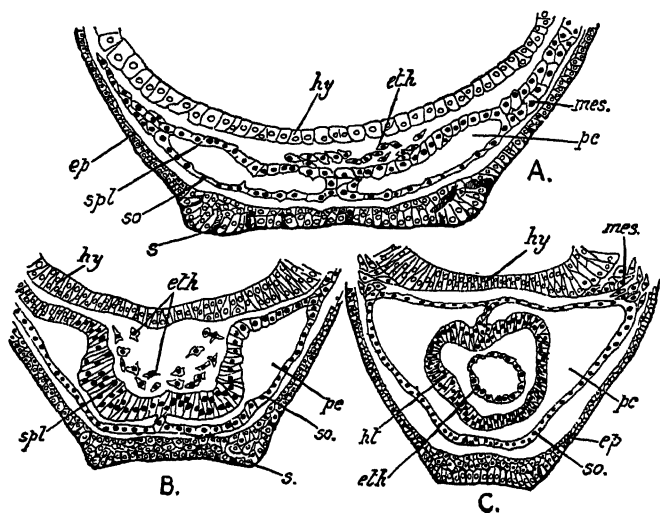


FIG. 284.—A, B, and C, transverse sections through the ventral wall of the throat of frog embryos of different ages, showing successive stages in the development of the heart.—From Bourne.

ep., Epiblast; *hy.*, hypoblast; *mes.*, mesoblast; *eth*, endothelial lining of heart; *ht.*, heart; *pc.*, pericardial cavity; *s*, sucker; *so.*, somatic layer of mesoblast; *spl*, splanchic layer of mesoblast.

tadpole, while it differs from the dogfish, resembles certain other fishes. When the lungs are formed, a vessel to supply each of them arises from the fourth efferent branchial vessel of the same side. Before the gills are lost, direct communication is established between the afferent and efferent vessels, so that when the gill capillaries disappear blood can pass direct from ventral to dorsal aorta through four continuous aortic arches. After the loss of the gill capil-

laries certain parts of the four arches disappear, while other parts persist and become the great arteries of the adult. The first branchial arch becomes the carotid. The portion of the suprabranchial artery which connected it with the

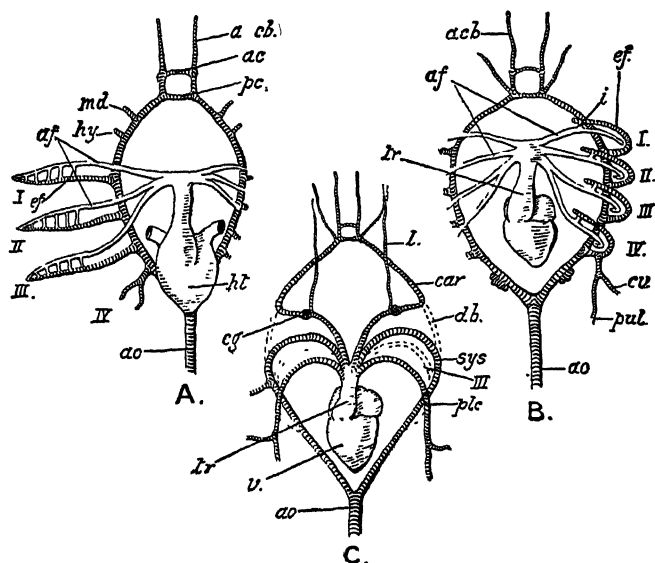


FIG. 285.—Diagrams of the heart and chief arteries of a tadpole.—
From Bourne.

A, The vessels of a tadpole at the stage when three external gills are present; B, the arrangement when secondary gills are in use; C, the adult arrangement.

a.c., Anterior commissural vessel, a.c.b., anterior cerebral artery, af., afferent branchial arteries; ao., dorsal norta, car., carotid artery; c.g., carotid gland; cu., cutaneous artery; d.b., ductus Botalli; ef., efferent branchial arteries; ht., heart; hy., efferent hyoidean artery; i., connecting vessel; l., lingual artery; md., efferent mandibular artery; p.c., posterior commissural vessel; p.l.c., pulmo-cutaneous arch; pul., pulmonary artery; sys., systemic arch, tr., truncus arteriosus; v., ventricle; I-IV, branchial aortic arches.

arch behind it is usually obliterated, but sometimes there remains a trace of it known as the *ductus Botalli*. The second branchial arch becomes the systemic arch. The third branchial arch disappears altogether. The fourth branchial arch becomes the pulmo-cutaneous. It loses its

connection with the aorta. In newts this connection persists, and is known as the *ductus arteriosus*. We have seen that it is present also during the development of the rabbit, where a vestige remains in the adult.

The first rudiment of the excretory system appears some time before hatching as a longitudinal thickening of the somatic layer of mesoblast on each side of the body, at the front end of the peritoneal cavity, immediately below

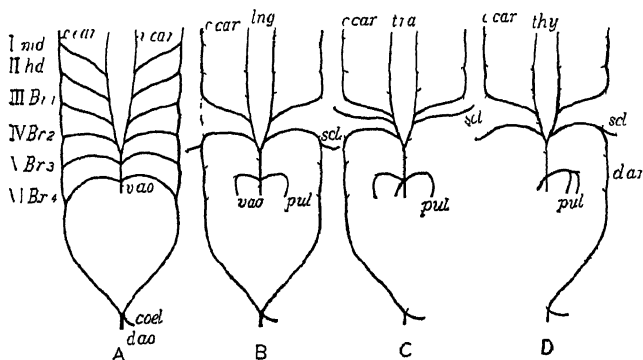


FIG 286 — Diagrams showing how the arterial systems of adult vertebrates are related to that of the embryo

A Theoretically complete system of arches not found in this form in any vertebrate adult or embryonic B, the system of the adult frog, C, that of the adult bird, D, that of the adult mammal

I-VI, Visceral arches Br 1-Br 4, branchial arches c car, common (dorsal) carotid cœl cœliac d ao, dorsal aorta dar, ductus arteriosus hd, hyoid arch ling, lingual representing ventral carotid md, mandibular arch pul, pulmonary scl, subclavian thy, small vessel to thyroid representing ventral carotid of embryo tra, small vessel to trachea, representing ventral carotid v ao, ventral aorta

the myotomes. The front part of this thickening becomes converted into the head kidney or pronephros (p 290), which consists of three twisted tubules, each opening by a funnel into the body cavity. Opposite the funnels a sacculated outgrowth of the splanchnic layer appears. It is known as the *glomerulus*¹ and becomes filled with blood from the systemic arch. The hinder part of the thickening which forms the

¹ Better as the *glomus*, a glomerulus being a small glomus for a single tubule

pronephros becomes a longitudinal tube, the *segmental duct*, into which the pronephric tubules open at their outer ends. This duct grows backwards and at the time of hatching opens into the cloaca. Some time later the mid-kidney or mesonephros arises as a series of paired masses of cells along the inner sides of the segmental duct, behind the pronephros. This part of the duct becomes the Wolffian duct. Each of the masses in question develops into one

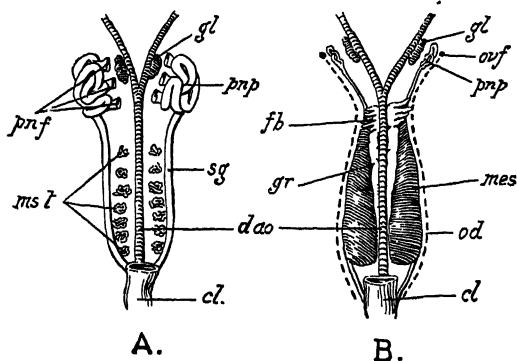


FIG. 287.—Diagrams of the development of the excretory system of the frog.—From Bourne.

A, The system of a tadpole about 12 mm long, showing the pronephros and origin of the mesonephric tubules; B, the system at the end of metamorphosis. The broken line represents approximately the position of the strip of peritoneal epithelium which gives rise to the oviduct

cl., Cloaca, d.ao, dorsal aorta; fb, fat body, gl., glomerulus; gr., genital ridge; mes., mesonephros; ms.t., mesonephric tubules, od, oviduct, ovf., position of oviductal opening, pnf., pronephric funnels; pnp., pronephros; sg, segmental duct.

of the tubules of the kidney, acquiring at one end an opening to the Wolffian duct and at the other a glomerulus and a nephrostome. Just before metamorphosis the pronephros and the front part of the segmental duct degenerate. The oviduct arises as a structure called the *Mullerian duct*, which is present in the late tadpole in both sexes, but degenerates in the male, leaving only a minute vestige. It is formed as a longitudinal tract of the peritoneal epithelium outside the kidneys, which becomes converted into a canal, the front part by being

grooved and then closing in, the hinder part by hollowing out. Part of the groove does not close, but remains as the internal opening of the oviduct. The gonads are formed as thickenings of the coelomic epithelium, one on either side of the mesentery, on the dorsal wall of the peritoneal cavity. No distinction between the sexes can be seen until the metamorphosis takes place.

The difference in the segmentation of the ova of the lancelet and the frog is due to the presence in the latter of a considerable

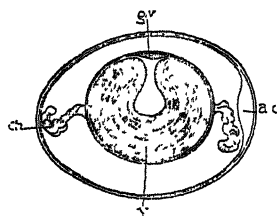


FIG. 288.—A diagrammatic section of the egg of a bird.—From Thomson.

a.c., Air chamber; *c.h.*, twisted cords in the white known as "chalazæ"; *g.v.*, small patch of protoplasm comparatively free from yolk, in which lies the "germinal vesicle" or nucleus, *y.*, yolk, in alternate layers of yellow and white substance. The yolk is surrounded by the "white of egg." Note the two membranes underlying the shell and separating to enclose the air chamber.

Kinds of Segmentation.

quantity of yolk or food material stored to provide for the nourishment of the embryo during the early stages of development. This yolk, lying on one side of the egg, hampers the relatively scanty protoplasm there, so that it divides more slowly. In the dogfish and in birds the yolk is still more plentiful, with the result that the portion of the egg in which it is stored never divides at all, but remains as an inert mass until it is surrounded by the growth of the small protoplasmic region or *germinal disc* which lies originally at one pole, containing the nucleus and segments

to form the cells of the embryo. The segmentation of the ovum of the lancelet is *complete or holoblastic* and almost *equal*; that of the ovum of the frog is holoblastic and *unequal*; in the dogfish and in birds it is *incomplete or meroblastic*.

Segmentation of the egg of a bird, such as the common fowl, begins with the formation across the germinal disc of a furrow which does not quite reach its edge. This is soon crossed by another furrow, and then more appear till the disc is divided into a mosaic of small irregular segments. Sections of the disc show that at the same time horizontal clefts are

Development of the Chick.

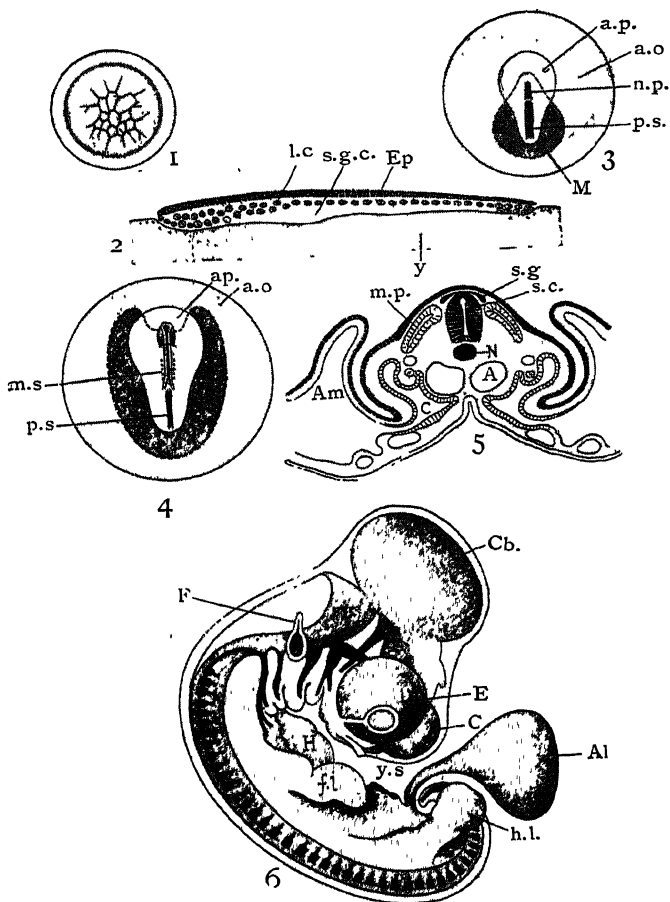


FIG. 289.—Stages in the development of a chick.—After Marshall.

1. Segmentation, superficial view of blastoderm. 2. Vertical section of blastoderm. *Ep.*, Epiblast; *l.c.*, lower layer of cells; *s.g.c.*, sub-germinal cavity; *y.*, yolk. 3. Diagrammatic surface view. *a.p.*, Area pellucida; *a.o.*, area opaca; *n.p.*, neural groove; *p.s.*, primitive streak; *M.*, mesoblast spreading over yolk. 4. Diagrammatic surface view of later stage. *a.p.*, Area pellucida; *a.o.*, area opaca; *m.s.*, mesoblast segments; *p.s.*, primitive streak. The dark border shows the spreading of the mesoblast over the yolk. 5. Cross-section. *s.c.*, Spinal cord; *s.g.*, rudiment of spinal ganglia; *N.*, notochord; *m.p.*, muscle plates; *A.*, norta; *Am.*, amnion fold; *c.*, coelom or pleuro-peritoneal cavity. 6. Embryo. *Cb.*, Cerebellum; *H.*, ear; *f.l.*, fore-limb; *h.l.*, hind-limb; *y.s.*, stalk of cut-off yolk sac; *Al.*, allantois; *E.*, eye; *C.*, cerebrum. On the dorsal surface the mesoblastic somites are indicated.

forming, by which the segments become separated from the underlying yolk. By a further series of clefts the disc then becomes two or three cells deep. In this way, shortly before the laying of the egg, a cap of cells known as the *blastoderm* is formed. In this the upper layer, the *epiblast*, is separated by a chink, the *blastocoele*, from a deeper mass of *lower layer cells*, from which the *hypoblast* and *mesoblast* will arise. The first rudiment of the

enteron appears as a space formed by the separation of the lower layer from the underlying yolk, known as the *sub-germinal cavity*. In a surface view of the blastoderm this gives rise to a central translucent *area pellucida*, round which is the *area opaca*, where the edge of the blastoderm rests on the yolk. The blastoderm grows over the yolk, the epiblast extending by the division of its cells, the lower layer partly in this way, partly by the addition of new cells cut off from the yolk. The blastopore is represented by a longitudinal strip in the hinder part of the blastoderm, where the epiblast is thicker than elsewhere and remains longer in continuity with the lower layer. This is the *primitive streak*, and is marked by a

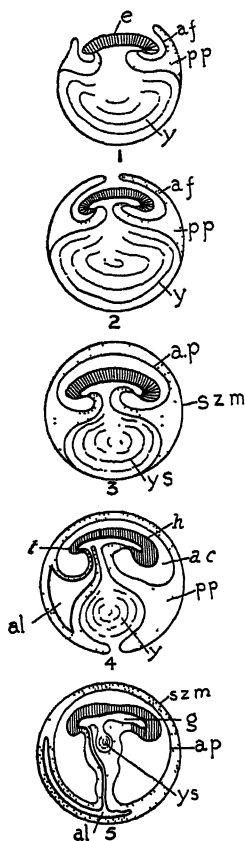


FIG. 290.—The origin of amnion and allantois.—After Balfour.

- 1 Rise of amniotic folds (*af.*) around embryo (*e*); *p.p.*, pleuro-peritoneal cavity or coelom; *y*, yolk.
- 2 Further growth of amniotic folds (*af.*) over embryo and around yolk.
- 3 Fusion of amniotic folds above embryo, *ap*, amnion proper; *s.z.m.*, false amnion or sub-germinal membrane; *y.s.*, yolk sac.
- 4 Outgrowth of allantois (*al.*); amniotic cavity (*ac*); *h.*, head end; *t.*, tail end.
- 5 Complete enclosure and reduction of yolk sac (*y.s.*); *s.z.m.*, sub-germinal membrane, *ap*, amnion proper, *al.*, allantois; *g.*, gut of embryo.

longitudinal *primitive groove*. The formation of the organs of the chick cannot be followed here. In broad outline it takes place in the same way as in the frog. Something must be said, however, about the *folding off of the embryo* and the formation of the *embryonic membranes* which are found in reptiles, birds, and mammals. As development proceeds folds appear in the blastoderm of the area pellucida around a region which is forming the embryo, beginning in front and behind as *head and tail folds* and afterwards joining at the sides. By these the little embryo proper is constricted off from the yolk, which is enclosed in a yolk sac formed by the growth round it of the blastoderm. As the embryo grows and absorbs the yolk it becomes larger than the yolk sac. The *amnion* is a peculiar membrane which envelops the embryo and arises in the following way. At a time when the splitting of the mesoblast into somatic and splanchnic layers has progressed some way outwards from the embryo over the yolk, there arises a fold parallel with that which formed the embryo, but consisting of somatopleure only. The folds on all sides of the embryo arch upwards and unite above, forming a dome over the embryo. Each fold is, of course, double. When they unite, the inner limbs of the folds form the *true amnion*, the outer limbs form the *false amnion*. The cavity bounded by the true amnion contains a fluid which bathes the outer surface of the embryo; that between the true and false amnions is lined by mesoblast and continuous with the coelom of the embryo. As the split between the layers spreads round the yolk sac, the outer layer it forms continues the false amnion, which finally encloses the sac. Meanwhile the folding off of the embryo has narrowed the stalk of the yolk sac, so that the amniotic cavity encloses the embryo except in the region of this narrow stalk in the middle of the belly. While the amnion is being formed, a sac known as the *allantois* grows out from the hinder part of the gut of the embryo. This is lined with hypoblast and covered with splanchnic mesoblast, and projects into the body cavity. It grows down the stalk of the yolk sac and spreads out between the true and false amnions. It becomes very vascular, and by its means the embryo breathes through the porous shell. The embryo chick has

gill clefts, and a system of arterial arches like that of the tadpole, but never shows any trace of gills. Finally, the beak pierces its way into an air chamber which exists at one end of the egg between the two membranes, and the animal begins to breathe by means of its lungs. The allantois now shrivels up (the yolk sac has already been absorbed) and the chick breaks its way out of the egg.



FIG. 291 —View of embryo with its foetal membranes
—After Kennel

am, Amnion proper *y*, dwindled yolk sac *al*, allantois *al*, subamniotic membrane *v*, villi. Outside the subamniotic membrane there is the delicate ectodermic trophoblast (*sch*)

In all mammals except the Monotremata the egg is minute and undergoes total segmentation. There is, however, no invagination such as is found in *Amphioxus*, but a stage comparable to the gastrula arises by the separation of layers of cells. It is covered with a layer formed from the outer epiblast cells known as the *trophoblast*. Outgrowths or "villi" of this burrow into the wall of the uterus, in which the embryo lies. The general course of development resembles that of the chick, a yolk sac, amnion, and allantois being

Development
of Mammals

formed. For a while the yolk sac forms a union with the uterine wall and serves for nutrition and respiration, but this is soon replaced by the allantois, which, as in the chick, spreads out under the false amnion or *subzonal membrane* and fuses with it. The organ thus formed is the placenta, and from it outgrowths penetrate into the uterine wall, expanding the original villi of the trophoblast and obtaining nourishment and exchanging gases with the maternal blood in lacunæ which are formed around them by the breakdown of blood vessels in the wall of the uterus. The navel of the adult marks the site of the *umbilical cord*, in which the stalk of the yolk sac and allantois and their blood

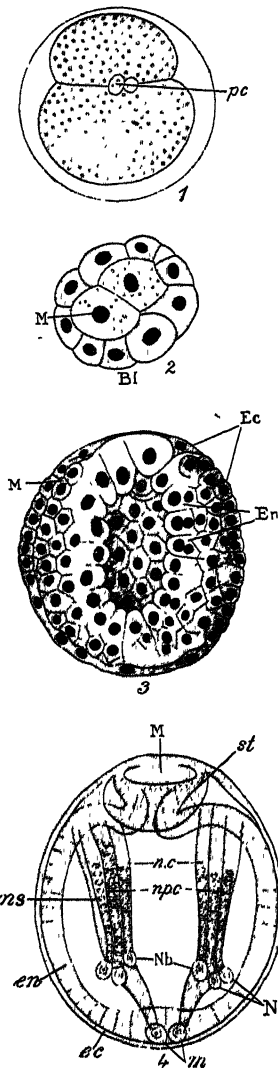


FIG. 292.—Stages in the development of an earthworm.—After Wilson.

1. Stage of two blastomeres; *pc*, polar bodies.
2. Blastula; *M*, primary mesoblast cell.
3. Gastrula in ventral view; *Ec*, ectoderm or epiblast; *En*, endoderm or hypoblast; *M*, mesoblast.
4. Late gastrula in ventral view, showing the bands of cells known as "germ bands"; *M*, mouth; *ms*, primary mesoblast cells; *ms*, mesoderm bands; *N*, nephridioblasts, large cells derived from the ectoderm which add to the bands of nephridial cells as the embryo lengthens; *Nb*, neuroblasts, similar cells at the ends of the bands of cells which form the nerve cords; *n.c.*, nerve cords, *npc*, cells which will form nephridia, *st*, stomodæum.

vessels entered the body. The amnion is the "caul," and the placenta is shed as the "afterbirth."

In the earthworm and the swan mussel the segmentation of the ovum is complete but unequal, and **Development of Invertebrates.** forms a hollow blastula, which invaginates to give rise to a gastrula. The mesoderm arises as two bands along the ventral side formed by the division of a pair of *pole cells* at the hind end. In the crayfish the segmentation is incomplete, but of a different kind from that of the chick and dogfish. The nucleus divides till a number of daughter nuclei are formed, and these migrate to the surface, where they are at first embedded in a continuous sheet of protoplasm which encloses a central mass of yolk. Afterwards this protoplasm segments to form a one-layered blastoderm enclosing the yolk mass. Thus there arises a sort of blastula which has no blastocoele, but contains yolk. A shallow invagination on one side of this gives rise to a gastrula with a small enteron. The mesoderm arises as two ventral bands, though pole cells are not found. The later stages of development in these animals cannot be followed here, but it may be stated that it is quite unlike that of the vertebrata.

A comparison of the processes that have just been described shows two facts of importance. (1) They all have certain features in common. (2) The animals which are more alike as adults resemble one another longer in development. This generalisation is known as *von Baer's law*. All animals have at one stage no body nuclei. All Metazoa pass later through a gastrula stage of two layers only. When the Triplobastica acquire a third layer, this happens in one way in all Chordata, and in another in the three non-chordate forms we have studied. All Chordata have at one stage a series of mesoblastic somites on the dorsal side of the gut, a notochord, a hollow dorsal nervous system formed by the folding of a neural plate, and gill-clefts. All Vertebrata have at a later stage a cartilaginous skeleton and a circulatory system like that of a fish. At a later stage still, the frog, bird, and mammal have pentadactyle limbs and the rudiments of lungs. The embryo of a rabbit is at one stage much like that of many

other mammals, then it takes on the features of a rodent, finally it shows those of its own species. At the same time it must not be overlooked that von Baer's law holds good only in a very general sense. The resemblance between the young stages of related animals is never exact and is often greatly obscured by disturbing factors, such as variations in the amount of yolk present or the precocious development of certain organs. Thus, for instance, the amnion and allantois which are peculiar to reptiles, birds, and mammals are developed at an exceedingly early stage, when the embryo is only beginning to take on the features which are common to all chordate animals.

CHAPTER XXIII

CLASSIFICATION AND EVOLUTION

THE animals that we have examined in the foregoing chapters have been chosen with a view to **Classification :** their serving, among other things, as examples **Species.** of the principal kinds of creatures that constitute what is known as the Animal Kingdom. Explicitly or implicitly, the study of different objects of any kind must always proceed by a recognition of their resemblances and differences, but the number of different kinds of animals is so enormous that it is quite impossible to study them without arranging them in an orderly classification according to their degrees of likeness. We have seen that no two individual animals are wholly alike. The offspring of any parent are always unlike it and unlike one another. Even so-called "identical twins," whatever may be the case at their birth, become to some degree different by the different action of their surroundings upon them as they grow up. Heredity, in fact, does not produce absolute resemblance, but is qualified by what, using the term in its widest sense, we may call *variation*, whether it be due to an unlikeness in the offspring at birth or acquired by the impress of the surroundings during their lifetime. At the same time, the likeness between the offspring of any parent is, on the average, greater than their likeness to individuals descended from other parents, and in this fact we find the first degree of resemblance between animals. For practical purposes, however, the resemblance between members of a family (in the ordinary sense of the word) is useless in classification, on account of the vast number of small divisions it gives and the impossibility of identi-

lying them. A more practicable basis is found in the fact that animals which are closely alike will breed together and give fertile offspring, whereas those which are less alike will not. Thus the offspring of two horses is fertile, but that of a horse and an ass is not, while breeding between horses and oxen is impossible. The primary groups of zoological classification consist of individuals which will breed together to give fertile offspring, or of which it is concluded from their likeness that they could do so. Such a group is known as a *species*. It is believed that all the members of a species are united by blood kinship; that is to say, that they are all in the long-run the descendants of one pair or several related pairs of parents, so that their relationship is only an extension of that which exists between offspring of the same parents. Thus the resemblance between the members of a species depends on two things: (1) their community of descent, (2) their inability to weaken their likeness by interbreeding with unlike kinds of animals and thus acquiring new features. At the same time it must not be overlooked that upon the average, two members of a species differ in more respects than two children of one parent.

Species are grouped together by zoologists into divisions of a higher grade known as *genera*. A genus consists of several species which resemble one another closely, but its limits are determined by convenience only, and are not natural, like those of a species. To every species there is assigned a Latin name consisting of two words, of which the first denotes the genus to which the species belongs, while the second is peculiar to the species. Thus the generic name of the rabbits and hares (p. 333) is *Lepus*, the specific name of the rabbit is *cuniculus*, the common hare is *Lepus timidus*, the mountain hare *L. variabilis*. We have seen similar cases in the species of the genera *Hydra* (p. 139) and *Astacus* (p. 206). The Latin names of many species are arbitrary, and some are even misleading, but they have the advantage of providing a generally recognised, international nomenclature. In the foregoing pages the Latin name of each species has been given. Above the genus are many divisions of the same nature, but higher rank.

Higher
Groups.

Genera are grouped into *families*, these into *orders*, orders into *classes*, classes into *phyla*, and in many cases it has been found necessary to institute additional grades of division, such as subclasses, subphyla, etc. The systematic position of the frog will serve as an instance of this arrangement. The frog is the Species *R. temporaria*, the Genus *Rana*, Family *Ranidae*, Order *Anura*, Class *Amphibia*, Subphylum *Vertebrata*, Phylum *Chordata*, Grade *Triploblastica*, and Subkingdom *Metazoa*. The following Table shows the main lines of the classification of the animal kingdom :—

I. Subkingdom PROTOZOA.

Animals whose bodies have not a cellular structure.

Contains only the :

Phylum PROTOZOA.

a. Class GYMNOXYXA.

Protozoa which move by means of pseudopodia.

e.g. *Amœba*, *Pelomyxa*.

b. Class FLAGELLATA.

Protozoa which move by means of flagella.

e.g. *Polytoma*.

c. Class CILIATA.

Protozoa which move by means of cilia and have nuclei of two kinds.

e.g. *Paramecium*, *Vorticella*, *Carchesium*.

d. Class SPOROZOA.

Protozoa which are always internal parasites, form numerous spores, and have often no external organs of locomotion.

e.g. *Monocystis*.

II. Subkingdom METAZOA.

Animals whose bodies have a cellular structure.

A. Grade DIPLOBLASTICA.

Metazoa in whose bodies there are only two protoplasmic layers, ectoderm and endoderm. Contains only the :

Phylum CœLENTERATA.

Radially symmetrical, diploblastic animals. The most important members of this group are :

Class HYDROZOA.

Polyps and medusæ with ectodermal gonads and no partitions in the enteron.

e.g. *Hydra*, *Obelia*.

Class ACALEPHÆ.

Medusæ with endodermal gonads and with a gullet and vertical partitions in the enteron of the polyp stage when the latter exists.

The large Jelly-fish belong to this group.

Class ANTHOZOA.

Polyps without a medusoid generation and with endodermal gonads, a gullet, and vertical partitions in the enteron.

Here belong Sea Anemones and Corals.

B. Grade TRIPLOBLASTICA.

Metazoa in whose bodies a third layer, the mesoderm, lies between ectoderm and endoderm and usually contains spaces known as the hæmocœle and cœlom.

1. Phylum PLATYHELMINTHES.

Flat, worm-like Triploblastica without anus, blood vessels, or (in the adult at least) body cavity, with an excretory system formed of branched tubes ending in flame-cells, and with a complicated, usually hermaphrodite system of reproductive organs.

a. Class TURBELLARIA.

Free-living, ciliated Platyhelminthes.

e.g. *Planaria*.

b. Class TREMATODA.

Parasitic Platyhelminthes with a cuticle, a forked gut, and no proglottides.

e.g. *Distomum*.

c. Class CESTODA.

Parasitic Platyhelminthes with a cuticle, no gut, and proglottides which break off from the body.

e.g. *Tœnia*.

2. Phylum ANNELIDA.

Bilaterally symmetrical, segmented Triploblastica, with a closed blood-vascular

system, a well-developed coelom, a double ventral nerve cord parting in front to enclose the gut, and a thin cuticle.

a. Class OLIGOCHÆTA.

Annelida without parapodia, with setæ.

e.g. *Lumbricus*.

b. Class POLYCHÆTA.

Annelida with parapodia and numerous setæ.

e.g. *Nereis* and *Arenicola*.

c. Class HIRUDINEA.

Annelida without parapodia or setæ, with two suckers, and with canalicular coelom.

Leeches.

3. Phylum ARTHROPODA.

Bilaterally symmetrical, segmented Triploblastica with an open blood - vascular system, a very restricted coelom, a double ventral nerve cord parting in front to enclose the gut, a thick cuticle, and paired, jointed limbs, some of which serve as jaws.

a. Class CRUSTACEA.

Aquatic Arthropoda with gills and two pairs of antennæ.

e.g. *Astacus*.

b. Class HEXAPODA OR INSECTA.

Land Arthropoda without gills, but with internal air tubes for breathing, with one pair of antennæ, three pairs of legs, and usually two pairs of wings.

The characteristic features of the following groups of insects and examples of their members are given in Chapter XV.

Orders: ORTHOPTERA, NEUROPTERA, COLEOPTERA, HYMENOPTERA, HEMIPTERA, DIPTERA, LEPIDOPTERA.

c. Class MYRIAPODA.

Land Arthropoda without gills but with internal air tubes, with one pair of antennæ, numerous pairs of legs, and no wings.

Centipedes and Millipedes.

d Class ARACHNIDA

For the most part land Arthropoda without gills, but with internal air spaces, and all without antennæ and with four pairs of legs
Spiders, Scorpions, etc

4 Phylum MOLLUSCA

Bilaterally symmetrical, unsegmented Triploblastica with an open blood - vascular system, a perivisceral coelom of moderate size, a nervous system which encircles the forepart of the gut, a shell, but no cuticle, a mantle fold, and a ventral, muscular foot
e.g. *Anodonta* Snails and Cuttlefish
also belong to this phylum

5 Phylum ECHINODERMATA

Radially symmetrical, marine Triploblastica without true blood vessels, with a spacious, complicated coelom, and with calcareous plates in the dermis
Starfish, Sea-urchins, etc

6 Phylum CHORDATA

Bilaterally symmetrical, usually segmented Triploblastica, with a closed blood-vascular system, a spacious coelom, a hollow, dorsal central nervous system, a notochord, and gill-clefts

a Subphylum CEPHALOCHORDA

Chordata with a notochord which runs from end to end of the body and lasts throughout life, an atrium, and very numerous gill-slits provided with tongue bars, without definite brain, heart, limbs, or skeleton of bone or cartilage
e.g. *Amphioxus*

β Subphylum VERTEBRATA

Chordata in which the notochord does not reach the front of the head and is usually reduced or lost in the adult, without atrium, with few gill-slits, which are without tongue-bars and are often lost in the adult, with well-developed brain, heart, usually two

pairs of limbs, and always an internal skeleton of bone or cartilage.

a. Class PISCES.

Cold-blooded Vertebrata with paired fins, bony scales, rays in the median fins, persistent gill-clefts, and no lungs, amnion, or allantois. The most important divisions are :

Order ELASMOBRANCHII.

Cartilaginous fishes without an air-bladder.
e.g. *Scyllium*.

Order TELEOSTOMI.

Fishes with bone in the skeleton and an air-bladder.

Sturgeon, Salmon, Cod, Herring, Plaice, and most fishes.

b. Class AMPHIBIA.

Cold-blooded Vertebrata with pentadactyle limbs, usually no scales, no rays in the median fins, lungs, shell-less eggs, no amnion or allantois, and a tadpole larva, with gill-clefts which are usually lost in the adult.

e.g. *Rana*. Newts belong here.

c. Class REPTILIA.

Cold-blooded Vertebrata with pentadactyle limbs, horny scales, no median fins, lungs, large, heavily yolked eggs laid in calcareous shells, no larva, an amnion and an allantois in the embryo, and the gill-clefts never functional.

Lizards, Snakes, Turtles, and Crocodiles.

d. Class AVES.

Warm-blooded Vertebrata with pentadactyle limbs, of which the first pair are wings, feathers and on the legs horny scales, no median fins, lungs, large, heavily yolked eggs laid in calcareous shells, no larva, an amnion

and an allantois in the embryo, and the gill-clefts never functional.

Birds.

e. Class MAMMALIA.

Warm-blooded Vertebrata with pentadactyle limbs, hairs, but no scales, median fins only in some whales, where they have no rays, lungs, eggs almost always minute, developing within the mother, milk-glands, no larva, an amnion and an allantois in the embryo, and the gill-clefts never functional.

The characteristic features of the following groups of mammals are stated and examples of their members mentioned in Chapter XXI.

- i. Sub-class PROTOTHERIA.
Order MONOTREMATA.
- ii. Sub-class METATHERIA.
Order MARSUPIALIA.
- iii. Sub-class EUTHERIA.
Order CEFACEA.
Order EDENTATA.
Order SIRENIA.
Order UNGULATA.
Sub-order ARTIODACTYLA.
Tribe SUINA.
Tribe RUMINANTIA.
Sub-order PERISSODACTYLA.
Sub-order PROBOSCIDEA.
Sub-order HYRACOIDEA.
Order RODENTIA.
Order CARNIVORA.
Order INSECTIVORA.
Order CHIROPTERA.
Order PRIMATES.
Sub-orders : LEMUROIDEA, ANTHROPOIDEA.

The discovery of differences such as those with which we have just been concerned is one of the main tasks of zoology, but it is not the whole task. As we saw in the first chapter, an essential part of the science is the attempt to explain the differences which it finds. The unlikeness between the several kinds of animals is not explained by the fact that in most, if not in all, cases it corresponds to

**The Meaning
of Differences
between
Animals.**

differences in their lives. A full explanation of it can only be reached when we know both how it has arisen and why it is connected with different modes of life.

From the earliest days of the science two theories have been current as to the origin of the differences between the several kinds of animals. One contents itself with the statement that each species has come into being independently by a process of *special creation*, whose method it does not attempt to explain. The other alleges that every species has sprung from some other species that was in existence before it, by a process known as *evolution*, which arises from the existence of differences between parents and their offspring, and that the differences upon which the zoologist founds genera and higher groups are due to the unlikeness between species being increased by the same process. Evolution is an alteration of the average characters, either of the whole of a species or of a certain group of its members, from generation to generation in a constant manner, by which they become so different from what they were at first that a new species arises. This theory is now held by all zoologists. It is based upon several classes of evidence. (1) It is supported by the facts upon which *classification* is based. Species, genera, families, orders, etc., are like the branches of a genealogical tree, and when they are arranged as such suggest strongly that they have arisen by modification each from the preceding grade. By the alteration in different directions of groups of members of a single species the several species of a genus would arise. As each of these pursued its own line of evolution it would become more unlike its congeners until it reached the rank of a genus, by which time it would generally have given rise to species of its own, and so forth. Every attempt to classify animals results in an arrangement which to some extent suggests the evolution of its members, but in modern zoology classifications are expressly so constructed as to show what are believed to have been the lines of evolution which animals have followed. Each of the groups of such a classification represents an original species, from which all the subdivisions of the group are supposed to have arisen by

descent with modification in various directions. As an illustration of this, the several groups of the classification of the Mammalia given in Chapter XXI. may be arranged in the form of a genealogical tree as follows:—

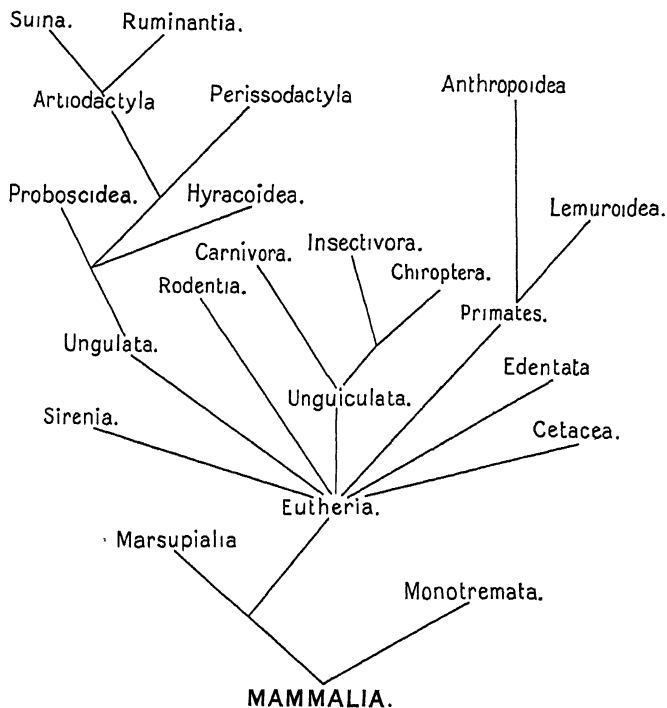


FIG. 293.—The classification of the Mammalia arranged in the form of a genealogical tree.

(2) The facts of *morphology* also support the theory of evolution. In our survey of a series of types of animals we have seen that they are all built upon the same general plan, which is modified in different directions in the several instances. The hands of a frog, a rabbit, a man, a horse,

and a bird are all built upon one plan, though the parts are of different shapes in the several cases. It is difficult to find any satisfactory explanation of this except evolution. Organs which are believed to have arisen by modification of identical organs in an ancestral animal are said to be *homologous*.¹ Thus the wings of a bird and a bat are homologous with one another and with the hands of a man and the paddles of a whale. Organs which have the same function, but have arisen independently, are called *analogous*. The wings of a bird and an insect or the legs of a rabbit and a crayfish are analogous. In the same class of evidence we may place the existence of *vestigial organs*, such as the ear muscles of man, which can only be satisfactorily explained on the supposition that they were functional in an ancestor. (3) The facts of *embryology* suggest evolution. We have seen that different animals pass through similar stages, and that animals which are more alike resemble one another longer during development. All animals have at one stage no body nuclei, all Metazoa have at a later stage two layers only, all Vertebrata at a still later stage have gill-clefts and a notochord, all mammals at a later stage yet are five-fingered, and so forth. The simplest explanation of these facts is that (for reasons into which we cannot enter) development is a very rough recapitulation of evolution. This deduction from von Baer's law is known as the *theory of recapitulation*. (4) The facts of *distribution* are yet another support for the theory of evolution. It is found that the animal populations or *faunas* of various parts of the world differ, that this is the case even when the climates of the two regions are so similar that animals native in one will flourish in the other, as in England and New Zealand, and that the difference increases with the inaccessibility of one from the other. These facts have no explanation in the theory of special creation, but are easily explained on the supposition that the course of evolution

¹ The term is extended to include the case of members of a series in one individual, such as the nephridia of an earthworm or the limbs of a crayfish, which are said to be *serially homologous* because they are built upon the same plan, so that the repetition of structure which is seen in them appears to be of the same nature as the repetition of the structure of an ancestor in its descendants

has been different in the two cases owing to different histories in past geological times (5) The facts of *palæozoology* (or the geological history of animals) are also in favour of evolution It is clear that this is the only direction in which we could look for a complete *proof* of the theory, since all the other evidence does no more than enable us to infer past history from present facts Unfortunately, owing to what is known as the *imperfection of the geological record*, such complete proof is impossible The unsuitability of the bodies of many animals for preservation owing to the absence of hard parts, the destruc-

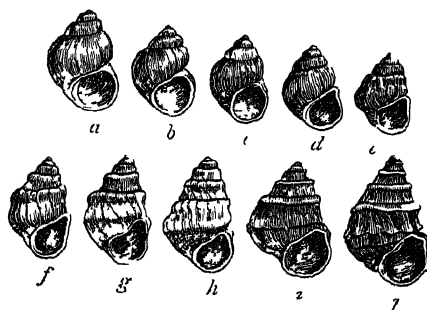


FIG 294 —The gradual transition between *Paludina neumayri* (a), the oldest form, and *Paludina harmeri* (j) —From Neumayr

tion of immense layers of rocks, and the small proportion of those which remain that can be examined, bring this about But it is established that throughout geological history there is a continual change in the types of animal life, leading up to those that exist at the present day, and in a few rare cases, particularly among Mollusca (Fig 294), it is possible to trace fully the evolution of species, while in others, such as those of horses and of elephants, the origin of higher groups can be followed in the appearance of successive genera (Fig 295)

As to how evolution has been brought about there is a conflict of opinion One theory supposes that the modifications which arise in each individual in the course

of its life, by its activity in response to the stimuli it receives from its surroundings or by the dwindling of certain of its organs from lack of use, are inherited in some degree by its offspring, and that the accumulation of such small modifications produces at length a different kind of animal. Thus, since it is known that one effect of cold upon a mammal is to increase the growth of its hair, the long fur of species which live in

The Process of Evolution : Lamarckism.

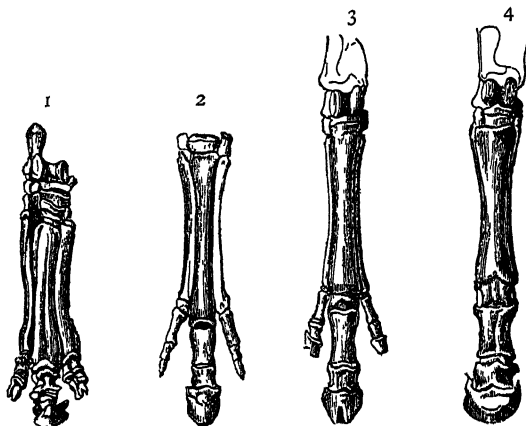


FIG. 295.—The bones of the foot of a horse compared with those of earlier members of its family.—After Neumayr.

- 1, Palæotherium, which appeared in the "Eocene" period of geology;
- 2, Anchitherium, which appeared in the following "Miocene" period;
- 3, Hippotherium, which appeared in the "Pliocene" period, 4, the modern horse. Note the continuous reduction of the side toes.

cold countries might be supposed to be due to the inherited effect of the climate. Again, the effect of use upon muscles is to increase their size, and in this way the great size of the wing muscles of birds of strong flight might be supposed to have been brought about in the course of many generations. On the other hand, the dwindling which is undoubtedly caused in the organs of individuals by disuse might in time bring about permanent degeneration, such, for instance, as that which is found in the eyes of animals which live in dark caves. This hypothesis is known as

the *Lamarckian theory*, from the name of its greatest exponent. It is not held by most zoologists at the present day on account of the lack of satisfactory evidence that modifications which are produced in the course of the life of an individual are transmitted by it to its offspring. Such modifications are known as *acquired characters*, and over the question of their inheritance discussion is still rife. The obstacles to belief in their transmissibility lie not only in the failure of numerous experiments and observations to prove it, but also in the difficulty of conceiving any way in which modifications in distant parts of the body can so affect the germ-cells as to be handed on to the offspring.

Another hypothesis as to the way in which evolution is brought about is the *theory of natural selection*, known as *Darwinism* after the great naturalist by whom it was formulated. It supposes that the transformation of species is caused by the destruction by adverse circumstances of certain kinds of individuals in each generation before they can breed.¹ The result of this will be that the next generation does not inherit the peculiar features of these individuals, which therefore gradually cease to appear in the species. Thus in a cold country those members of a species of mammals which had not thick fur would either die of cold or be so enfeebled that they could not compete with the rest in the struggle for food or mates, or in a herd of wild horses pursued by wolves the slowest would be killed, so that the next generation would be descended from those members of the species which were best clad or swiftest, as the case might be, and would of course inherit their peculiarities. The result of this process would be the selection by Nature of certain individuals to breed, just as a breeder selects sheep with thick wool or cattle with certain muscles well developed, and, breeding from these in preference to the rest, alters his breed of sheep or cattle. Evolution by natural selection depends upon three factors: variation, the struggle for existence, and heredity. (1) We have seen that all animals are

¹ Of course the eliminated individuals would not always be killed before they could breed. In some cases the reproductive period would merely be cut short so that the number of offspring was lessened.

variable It is true that there is great doubt of the heritability of the "acquired" variations¹ produced in the individual by the action of its surroundings at various stages of its existence, but there are other variations of whose inheritance there is no doubt. These are known as *germinal variations or mutations*, and are due to inborn tendencies which arise in the germs in some way which is not as yet understood. It is often urged that variations are too small to give an effective advantage in the struggle for existence, but mutations may be so great that in regard to them this difficulty does not exist. It may be that evolution takes place by the inheritance of such mutations alone.

(2) The *struggle for existence* is due to the fact that every animal produces more offspring than survive, because, while the offspring are always more numerous than the parents, the total number of individuals in the species does not as a rule increase, being already as many as the conditions of food, enemies, etc., will allow. A pair of robins will produce ten or more young in a year, yet, since the number of robins does not increase, only two of these can survive. This is an exceptionally small death rate. Many animals produce thousands of offspring. The blow fly, for instance, gives rise to a progeny of 20,000. Now it is impossible to believe that the destruction which this involves is altogether haphazard. Some of the individuals will be feebler, or slower, or less cunning, or less protectively coloured, or less warmly clad than the rest, and it is certain that these will as a rule be the first to be destroyed, and that the survivors will generally be above the average of the rest in regard to the characters in which selection has taken place.

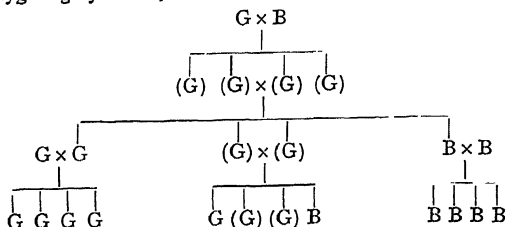
(3) The alteration which is thus made in the average characters of the species will be maintained by the action of *heredity*. It is often alleged as an objection to the theory of evolution by natural selection that any large variation in a favourable direction, though it may lead to the survival of the individual in which it occurs, will nearly always be weakened in the next

¹ Small acquired variations due to the effect of the environment during growth are known as *fluctuations*. Thus one of a litter of young being better nourished in the womb may be larger and stronger, but will not transmit those qualities to its offspring.

generation by what is known as the "swamping effect of intercrossing." That is to say, the exceptional individual will probably mate with an average member of the species and their offspring will be intermediate between them, and so in a few generations the favourable variation will have become so slight as to give no effective advantage in the struggle for existence. This difficulty, however, disappears in the light of discoveries which have been made by the students of heredity known as the *Mendelian* school after the discoverer of the principles upon which they rely. We have already seen that, in many cases, when two individuals which differ in any respect breed together, their features do not blend, but the peculiarity of one parent is "dominant" in the offspring, while that of the other is latent or "recessive." For instance, the offspring of a wild grey rabbit and the black variety are all grey. Thus the dominant variety remains distinct and is not weakened by crossing. If, however, the offspring of such a cross be bred together, it will be found that the recessive variety has also not been extinguished, for on the average a quarter of the offspring will throw back to the recessive grandparent (in this case, the black rabbit). Thus it comes about that both varieties remain unimpaired within the species, and either will have its effect on the survival of individuals in successive generations.

These facts are explained as follows. Each germ contains potentially all the characters of an adult organism. When germs unite the zygote therefore contains a double set of tendencies. In regard to each character, the germs may have been alike or unlike. If they were alike the zygote is called a *homozygote* and will show the character they both bore. If they were unlike the zygote is called a *heterozygote*, and one tendency becomes dominant over the other in its body-cells. At the reduction division in the formation of germs the tendencies again separate. In regard to the character in question, the germs of a homozygote will all be alike, those of a heterozygote will be unlike, consisting of equal numbers of both kinds. When heterozygotes breed together, on the average half the offspring will be formed by the union of unlike germs—that is, will be heterozygotes like their parents. Half the remainder will be homozygotes formed by the union of germs bearing the dominant character; half will be homozygotes formed by the union of recessive germs. All the dominant homozygotes and all the heterozygotes will develop the dominant character. All the recessive homozygotes will develop the recessive character. Thus three-quarters of the offspring will have

the dominant character, one quarter the recessive character. The recessives, if bred with recessives, will all breed true. Of the seeming dominants only one-third—those which are pure dominants—will breed true; the rest—the heterozygotes—will continue to throw one-quarter of pure recessives. In the following genealogical table G represents a homozygote grey rabbit, B a black, and (G) a heterozygote grey.



There are many difficulties in the way of the theory of evolution by natural selection: such, for instance, as the difficulty of explaining in this way the degeneration of useless organs, the rareness of variations of effective magnitude, the necessity for the simultaneous occurrence of many variations to originate or improve any organ, and so forth; but it is probable that in one form or another this theory is still held by the majority of zoologists. Some, however, unable to subscribe either to the Lamarckian or to the Darwinian theory, are compelled to fall back upon a belief in a directive force in the organism itself which compels it to change continuously in certain directions until it is extinguished by transgressing the limits which the conditions of life allow. Such a theory is in reality little more than an abandonment of the problem of adaptation. It does, however, emphasise a fact which upon other theories is apt to be forgotten, namely, that evolution is after all more the work of the organism than that of its environment. The organism alters, whether altogether spontaneously or as a result of its capacity to respond to changes in environment. The part of the environment is to decide which of the experiments of the organism are failures. By the two factors, the organism and its environment, each of the theories of evolution explains in its own way both the origin of species and their adaptation to such modes of life as are possible in their respective surroundings.

CHAPTER XXIV

THE ANIMAL IN THE WORLD

OUR survey of zoology is drawing to a close. We began with the discovery that an animal is an organism and with an attempt to realise what that fact means. We went on to examine a series of such organisms and to investigate the modes in which they have come into being both as individuals and as kinds of individuals. It remains for us to study briefly the relations in which these beings stand to other material things. The outstanding fact about an animal is that it is alive. Animals, however, are not the only things of which this is true. There are included among living beings many other creatures, of which the best known are the plants, though some cannot rightly be said to belong either to the animal or to the vegetable kingdom. We have now to find wherein lies the difference between these kinds of organisms and between the kinds of life which they exhibit. There is no fundamental difference in the composition of the protoplasm which is the essential part of all living things. Nor do they differ in the essentials of their life. This may be seen by comparing the activities of plants with those which we have studied in animals. That the protoplasm of plants is irritable we see in such cases as the turning of a sunflower towards the sun, or the stimulation by gravity of the stem to grow upward and the root downward, or the folding of the leaves of the Sensitive Plant (*Mimosa*) when they are touched. That it is automatic appears in such facts as the slow turning of the tendrils of climbing plants till they meet with objects to which they can cling. That it has conductivity can be seen when a stimulus given to the leaf

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between Living
Beings: Unity
of Life.**

of a mimosa causes distant leaflets to fold. That it can execute movements may in many cases be seen under the microscope, when it will be found to stream round the cell. That it makes substances by chemical activity and secretes them is illustrated by the long list of drugs and other substances obtained from plants. That it grows and reproduces need not be argued.

For all this agreement in essentials, however, there are between animals and plants distinctions which are both far-reaching and obvious. We may take our start from familiar notions on the subject. Any one who tried to state in words the ideas which he had unconsciously formed of animals and plants would probably find them to be somewhat as follows: An animal is a being that moves and feeds; a plant is a green thing that grows in the earth. Let us examine these notions. It will be best to base our analysis upon our definition of a plant. We find that the information it implicitly contains is: (1) That the plant is green, (2) that it does not swallow food, but draws nourishment from the earth (it is less generally known to obtain food from the air), (3) that it is fixed in one place and does not move about: usually, indeed, it does not move at all.

1. The green colour of plants is due to the presence of *chlorophyll* (p. 145). This is never found in animals, except in certain cases where minute green plants live embedded in the protoplasm of animal bodies, as in the green *Hydra*. At the same time it must be remembered that certain plants, such as the fungi, have no chlorophyll.

2. More important than the mere presence of chlorophyll is its function in the body, which is connected with the *nutrition* of the plant. We have already seen that this function is the obtaining of carbon from carbon dioxide by means of the energy of the sun's rays (p. 145), the carbon being caused to combine with the elements of water to form carbohydrates, and afterwards with nitrogen, sulphur, and phosphorus obtained in inorganic salts, to form more complex organic substances. From this peculiarity of nutrition arise several other features peculiar to the life of plants. (i) We have here the reason for the well-known fact that green plants cannot live in the dark. (ii) While

animals, as we have seen, are always taking in oxygen and giving out carbon dioxide, green plants in the light are continually taking in carbon dioxide and giving out oxygen. Yet it must be remembered that the protoplasm of plants undergoes continually a true respiration like that of animals, although this is obscured by the reverse process taking place to a greater extent during daylight. (iii) While the food of animals consists of complex organic substances, usually in the state of a solid or the viscous liquid protoplasm, and has to be swallowed through an opening, the materials taken in by green plants are simple inorganic substances which can be absorbed as gases or liquids through the surface of the body. We have seen, however, that plants which have no chlorophyll, such as fungi, and some animals which live as parasites or in decaying matter, absorb their nourishment through the surface of the body, but take it in the form of organic substances, more or less complex in various cases, from the living or dead bodies of other organisms.

3. From the mode of nutrition of plants there follows the third character which we have marked in them. In the great majority of animals food must either be sought by locomotion or at least seized by other *active movements*, as it is, for instance, in *Obelia* or *Vorticella*. In plants, on the other hand, not only is this necessity absent, but, since it is desirable that they should expose as great a surface as possible to air and water for absorption—as they do, for example, in leaves and roots—the shape of their bodies is necessarily such as to be an actual hindrance to motion. Thus in most plants active motion is restricted or absent, and muscular and nervous tissues are not found in plant bodies.

4. The necessity for surface leads to a fourth character in plants. An extensive surface needs strong support. In correspondence with this need we find in plants a massive skeleton which forms a strong wall to each cell, so that the protoplasm is upheld by an intricate framework of compartments whose walls are thickest in the most woody parts of the body. Owing, no doubt, to the ample supply of starch at the command of the plant, this skeleton consists of a modified form of starch known as *cellulose*. Among

plants, even including those like the fungi which have no chlorophyll, cellulose is almost invariably present; among animals it is unknown. It happens, indeed, that this comparatively unimportant character comes nearer than any other to giving an absolute distinction between the two kinds of organisms.

To sum up: we find between typical plants and typical animals the following distinctions:—

1. The presence in typical plants and not in animals of the green substance *chlorophyll*.
2. That while plants absorb through their surface simple inorganic compounds and from them *manufacture food-stuffs* for their protoplasm, animals swallow the complex substances of the bodies of plants and of other animals.
3. That while in plants *motion is restricted* or absent, it is conspicuous in animals.
4. That plants have a skeleton of *cellulose*, which is absent from the bodies of animals.

It will be seen that the differences between ordinary plants and animals are wide and striking. But the fact must not be overlooked that intermediate organisms are known. These are not such creatures as the sea anemones, which are true animals with the habit of remaining fixed in one spot, or the fungi, which are probably true plants that have lost their chlorophyll and consequently modified their mode of nutrition, so that they require somewhat more complex food materials. The real intermediate organisms are small creatures related to the Protozoa, which have the power of locomotion like animals, but possess like plants either chlorophyll or cellulose or both. Some of them can hardly be distinguished from the Flagellata. Their existence is a reminder that, fundamentally, all living beings belong to the same stock. In this connection must be mentioned the *Bacteria*, which are minute, rod-like or spherical organisms often classified with the plants, but of which it is probably more true to say that they are neither plants nor animals, but a third kind of living beings.

Euglena viridis, often so common in puddles as to give them a green colour, is an example of an organism intermediate between animals and plants. It is a minute, spindle-shaped creature, which may reach

**Organisms
Intermediate
between
Animals and
Plants.**

a length of $\frac{1}{2}$ mm. The front end is blunt and bears a flagellum rooted

Euglena

"gullet" but probably never used as such. There is a thin, horny cuticle, a distinct ectosarc, and a central, spherical nucleus. Arranged in bands, radiating from the nucleus, lie a number of oval, green bodies known as *chloroplasts*, which consist of dense protoplasm containing chlorophyll. Similar bodies are found in green plants. *Paramylum* granules are present, more numerous in sunlight. Waves of contraction like those of *Monocystis* pass along the body (Fig. 297), but there are no myonemes. The excretory system is complicated, consisting of a reservoir opening into the gullet, a contractile vacuole which discharges at intervals into the reservoir, and a number of accessory vacuoles which surround the main vacuole and re-form it. A red pigment spot or *stigma* lies against the front side of the reservoir and is said to enable the animal to appreciate the amount of light in its surroundings. Reproduction is by binary fission, beginning at the front end, the nucleus undergoing a peculiar mitosis. It may take place in free individuals after the loss of the flagellum, or in a gelatinous cyst, within which it may be repeated several times. A form of conjugation, with amoeboid gametes, has been reported in another species of *Euglena*. The nutrition of *Euglena* is normally holophytic, but the water must contain a little albuminoid matter. If the solution be rich in dissolved organic matter, the chloroplasts grow pale and shrink. In the dark this takes place with a lower percentage of organic matter, but in the absence of such matter the creature remains green even in the dark. Thus *Euglena* is holophytic and saprophytic. If it used its gullet for taking food it would combine all three forms of nutrition. It will be seen that in certain respects *Euglena* resembles *Polytoma*. There are other, nearer relations of *Polytoma* which contain chlorophyll, and it is interesting in this connection to recall that *Polytoma* itself is unlike most animals in forming starch. In fact, the position of a large number of Flagellata is doubtful as between the animal and vegetable kingdoms.

Here must also be mentioned some special kinds of metabolism which

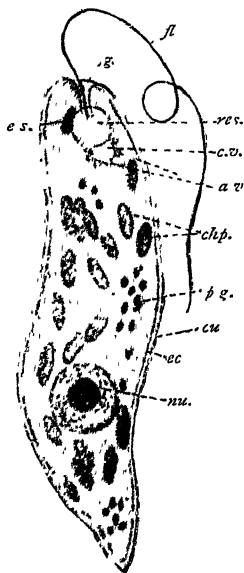


FIG. 296.—*Euglena viridis*, highly magnified.

a.v., Accessory contractile vacuoles; c.v., main contractile vacuole; cph., chromatophores; cu, cuticle; e.s., eyespot; ec, ectoplasm; fl., flagellum; g., gullet; nu., nucleus; p.g., paramylum granules; res., reservoir.

differ greatly, though not in principle, from the processes we have already traced. Certain organisms, such as the yeast fungus and many bacteria, are able to live without free oxygen, although they contain no chlorophyll to enable them to obtain it by the splitting of carbon dioxide. Such organisms are called *anaerobic*. They obtain their energy by the decomposition of oxygen-bearing molecules of a simpler and stabler sort than those which yield the energy of ordinary protoplasm. Thus the minute fungi of which yeast consists decompose grape sugar into alcohol and carbon dioxide according to the equation



with the evolution of so much energy in the form of heat that the temperature of the surrounding solution rises. This is the process of fermentation employed in the manufacture of alcoholic liquors, and from

it the term *fermentation* has been applied to other processes, such as the souring of milk or wine, in which an organism brings about a change in a mass of matter which is very great compared with that of its own body. It has been shown that in many such cases there is formed by the organism an enzyme (p. 49) which brings about the fermentation without itself being destroyed in the reaction. Such an enzyme has been found in

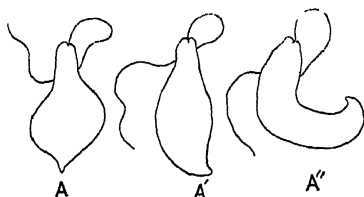


FIG. 297.—*Euglena viridis*.

A, A', A'', Three positions of the body.

the protoplasm of yeast. Quite a different class of fermentation is found in certain bacteria which obtain energy by the oxidation of inorganic substances, such as sulphuretted hydrogen, sulphur, ferrous salts, and ammonia. It is by an action of the latter class that the ammonia compounds excreted by animals, or resulting from the destruction of their bodies by putrefactive organisms, are converted into nitrates for the use of the higher plants.

The fundamental difference in nutrition between animals

The Balance of Nature.

and plants has an important result in regard to their relation with the rest of nature and with one another. In their action upon the inorganic world these two kinds of organisms bring about precisely opposite changes, and do so in such a way that each sets up conditions favourable to the activity of the other. The plant, absorbing the energy of the sun's rays, builds up with storage of that energy complex organic

compounds from simple inorganic substances.¹ These manufactured substances it assimilates, partly in repairing the waste of its protoplasm, but mainly in adding to its substance by growth. Its construction of organic materials is in excess of its destruction, and the net result of its activity is to provide an accumulation of those complex substances which form a necessary part of the food of protoplasm. At the same time it sets free oxygen. The animal, on the other hand, obtains the organic food for its protoplasm by consuming the substances manufactured by plants, either directly from the plant body or after they have been incorporated in a somewhat altered form into the protoplasm of other animals. In the protoplasm of the animal

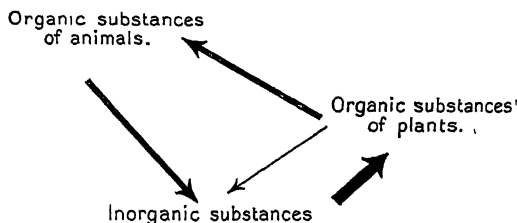


FIG. 298.—A diagram of the circulation of matter through the bodies of organisms.

these substances undergo destruction. Thus the animal destroys organic material without, like the plant, manufacturing from inorganic matter more to replace it. The net result of its life is to lessen the amount of organic matter in the world. At the same time it sets free carbon dioxide and simple nitrogen compounds. Thus plants provide food and oxygen for animals, while animals, destroying this food, provide simple nitrogen compounds² and carbon dioxide for the use of plants. The result is a *circulation of nitrogen and of carbon* through the bodies of organisms. It will be seen that this circulation of matter

¹ The storage of energy is of course due to the fact that more is absorbed in splitting the stable inorganic molecules than is freed in forming the unstable organic molecules.

² These are usually not available for the use of plants till they have been altered by the action of bacteria.

is accompanied by a transference of energy. The whole of the energy of the life both of plants and of animals is derived in the long run from the energy of the sun's rays stored by plants in the complex substances they manufacture. It is stored by plants: most of it is not set free till it reaches the bodies of animals. There is, of course, no circulation of energy. That which is set free from the bodies of organisms is lost to them, and has to be replaced by the fixing of more energy from the sun's rays by plants when they work up the excreta of animals.

The whole animal kingdom may be regarded as a vast

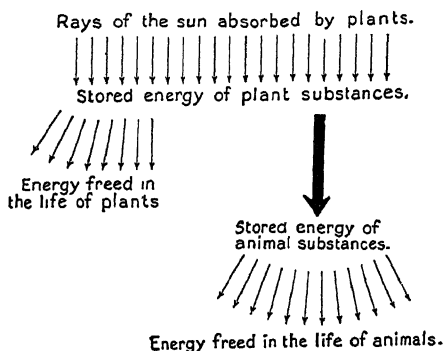


FIG. 299.—A diagram of the energy of organisms.

complex system which disposes of the material and energy accumulated by plants, by means infinitely more subtle than those which are possible in the inorganic realm. The relations between the different kinds of animals are based in the long-run upon nutrition. Either animals compete for the common supply of food which is derived directly or indirectly from plants, or some of them serve others for food, or in rarer cases they assist one another in the quest for food or in defence against enemies which would use them for food. We may class animals according to their food as omnivorous, herbivorous, and carnivorous, or according to their method of obtaining it as free living,

**Relations
between
Animals
based upon
Nutrition.**

parasitic, symbiotic, and commensal. Most of these classes need no further comment. We have seen instances of the ways in which omnivorous, herbivorous, and carnivorous animals obtain food. We have dealt briefly with parasitism and symbiosis. Under the head of *commensalism* a large number of curious instances of co-operation between animals is known. One of these must suffice here. The hermit crabs are crustaceans related to the crayfish, with the abdomen soft, owing to the thinness of its cuticle, and twisted so that it will fit into the empty shell of molluscs like the whelk. They search for such shells, often fighting one another for possession, so that they are sometimes called soldier crabs, and they anchor themselves into their shells by means of the limbs of the sixth abdominal segment. When they are attacked they withdraw into the shell by the contraction of a muscle in the abdomen, but often this does not save them from being eaten by fishes, of which they are a very favourite food. They are very active, and are constantly travelling in search of food, dragging about their shells with them. Sea-anemones are polyps related to *Hydra*, but more complicated in their internal structure. Owing to their

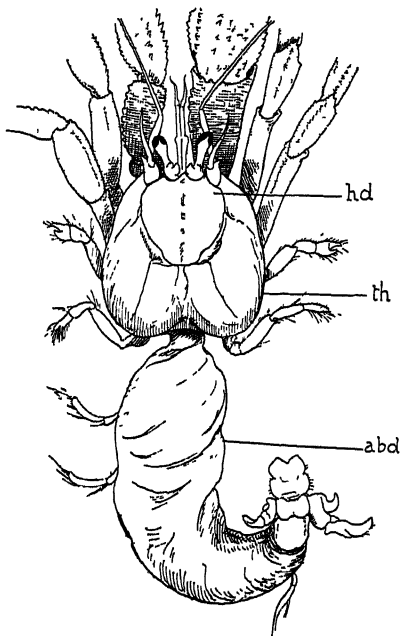


FIG. 300.—A hermit crab withdrawn from its shell. The anterior legs are broken.—From Thomson.

hd, Head; th, thorax; abd, abdomen.

parasitic, symbiotic, and commensal. Most of these classes need no further comment. We have seen instances of the ways in which omnivorous, herbivorous, and carnivorous animals obtain food. We have dealt briefly with parasitism and symbiosis. Under the head of *commensalism* a large number of curious instances of co-operation between animals is known. One of these must suffice here. The hermit crabs are crustaceans related to the crayfish, with the abdomen soft, owing to the thinness of its cuticle, and twisted so that it will fit into the empty shell of molluscs like the whelk. They search for such shells, often fighting one another for possession, so that they are sometimes called soldier crabs, and they anchor themselves into their shells by means of the limbs of the sixth abdominal segment. When they are attacked they withdraw into the shell by the contraction of a muscle in the abdomen, but often this does not save them from being eaten by fishes, of which they are a very favourite food. They are very active, and are constantly travelling in search of food, dragging about their shells with them. Sea-anemones are polyps related to *Hydra*, but more complicated in their internal structure. Owing to their

nematocysts they are distasteful to fishes, as is shown by the fact that they will not serve for bait. They cannot pursue food, but must wait till it comes within reach of their tentacles. Now certain kinds of sea-anemones are found on the shells of hermit crabs. Here they are never molested by the owner of the shell, and benefit by the constant change of feeding ground and by fragments of food which are let fall by the hermit crab, to obtain which some of them stand with the mouth on the lower side of the shell, which their base enwraps. In return the crab

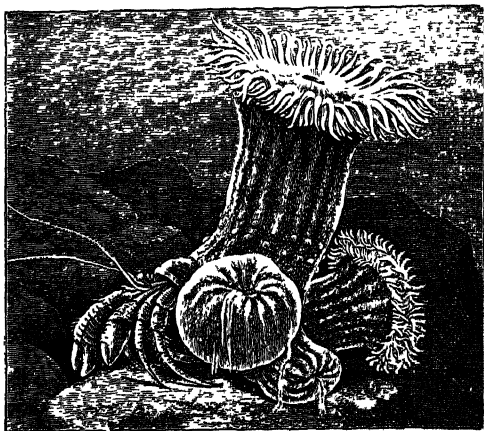


FIG. 301.—Sea-anemones on the shell of a hermit crab.
—After Andres.

obtains protection from fish, which are kept from eating it by the stinging powers of the anemone. Within the shell there is often found a species of *Nereis*, which with its horny jaws robs the food out of the very pincers of the crab, without, so far as can be seen, conferring any benefit in return, and must therefore be regarded as a parasite.

We have already briefly considered the relation in which living beings stand with their lifeless surroundings. We have seen that living protoplasm, delicate and unstable though it is, by a purposive reaction maintains its existence in the face of the great and unceasing changes of inorganic

nature, which would otherwise surely destroy it. In so doing it turns to its own use a part of the forces of nature, and this is the meaning of the circulation of matter and transference of energy through the bodies of organisms.

Only by a continual change of its substance can the organism keep in being. It is thus, like a stream or a whirlpool, an object in nature which remains in existence in spite of a continual change of its substance, but whereas the existence of the stream or the whirlpool is maintained by the action of external forces, the existence of the organism is maintained by a reaction in which energy is liberated and directed from within. The question suggests itself whether this behaviour on the part of living beings is due to their possessing any property that is not found in the rest of nature—whether, that is, life differs fundamentally from the processes of the lifeless world. This is the ultimate problem of Biology, and it brings us back to the consideration of those primary features of life with which we began our study of the animal organism.

1 *Irritability* is not peculiar to living beings. Any substance may be said to be irritable in which a change can be caused to take place by a stimulus whose magnitude bears no relation to that of the change it starts, and there is no lack of such substances among lifeless things. An instance that we have already used shows this clearly. Explosives disintegrate on the receipt of stimuli, and the firing of a gun by a slight pressure on the trigger is analogous to the performance of the movements which precede the firing, by a man on the receipt of such a stimulus as the sight of a bird.

2 In regard to *automatism* the position is less clear, and here no decision is possible until we know in what the automatism of living beings consists. A clock and a mass of radium are both automatic in the sense that each has an activity which is not directly dependent on external stimuli, but it does not follow that the automatism of a living being is of the same kind as that of either of these.

3 On the other hand, little reflection is needed to show that *disintegration with evolution of energy* is a common process in lifeless things. We have already seen,

for instance, that explosives respond to stimuli by disintegration. There remains, however, the possibility that, though the mere fact of disintegration with evolution of energy is not peculiar to living beings, the details of the way in which the freed energy appears may be so. The substance of the human body and that of a fire or a cartridge alike disintegrate with evolution of energy, but the way in which the energy appears is very different in the human body and in the other cases. Can we find in lifeless things processes comparable to those which are carried out by the energy of living matter? This is, of course, a separate problem in the case of each of the modes in which the energy is exhibited. It is not possible to discuss the question here, but we may say broadly that it is as yet unanswered. For instance, the most conspicuous case—that of movement—is due to the process known as contraction, in which, as we have seen, a portion of living substance changes in shape, though not in size, growing shorter in one direction, but wider in others. The claim is made that this process does not take place by internal activity in lifeless matter, but it has been shown that certain artificial emulsions (p. 112), when they are divided into small drops and placed in water, will move by their own activity, undergoing changes in shape which are alleged (though this is disputed) to be of the same nature as the contraction of living matter. In the same way secretion and excretion have not been explained by any process, such as filtration or osmosis, that takes place in lifeless matter, and it has been claimed, but is disputed, that such an explanation is impossible. On this point all that can be said at present is that no complete explanation of any of the processes in question has yet been given in terms of chemistry or physics.

4. The mere fact of the *incorporation* of new matter is not peculiar to living beings. Any liquid will take up into itself substances that are soluble in it. But we have seen that assimilation is the manufacture by living substance, out of unlike materials, of additional matter of its own composition. It has not yet been shown that this process is paralleled in any kind of lifeless substance. It is true that a suggestive analogy may be found in certain chemical re-

actions that take place with greater readiness in the presence of a trace of one of their products, which may then be said to assist in its own manufacture. In certain circumstances, for instance, the action of nitric acid upon copper is hastened by the presence of copper nitrate¹. But in such cases the presence of the substance helps rather than starts its own production, and the most that we can say is that there is a possibility that the same principle is involved here as in assimilation. In the light, however, of our present knowledge, we must regard assimilation as a property peculiar to living beings.

5 In regard to the processes which constitute *re production* it is again impossible to draw a parallel between living and lifeless things. (a) The case of fission is simpler than that of development. Drops of any colloidal solutions will in certain circumstances break up into droplets in a way that suggests the fission of those lower organisms whose whole body breaks up in reproduction into two or more apparently similar parts, and it is claimed, but disputed, that the process is the same in the two cases. We need not search, however, for analogies to fission among lifeless things. It is probably closely related to contraction, whose claim to be peculiar to the living body we have already seen to be as yet undecided. (b) One part of the problem of development may be dismissed in the same way as that of fission. The series of changes by which the adult is developed from the germ are but further instances of phenomena we have already discussed, such as growth and chemical change, and so far there is nothing new to us in development. But a complication is here introduced by the fact that the processes by which the germ develops *take place in such a way as to produce for the offspring a body of the same kind as that of the parent*. We have seen that the property to which this is due is called heredity. Now in heredity we do meet with a peculiarity of living things, though it is perhaps not immediately obvious wherein this peculiarity consists. (1) Heredity is not peculiar in that it enables a part of

¹ An instance of a reaction in which organic substances exhibit this phenomenon of "autocatalysis" is the hydrolysis of certain esters, which is aided by the presence of the free acid.

the body which is broken off to retain the properties of the mass from which it is broken. This is equally the property of any material body—as, for instance, of the droplets of quicksilver to which we have alluded. (ii) It does appear at first to be peculiar in that it enables a portion of matter to revert by its own activity to a structure which it formerly possessed. But the fact has been pointed out that something like this happens in various kinds of lifeless matter. A mass of plastic sulphur, for instance, will in time revert to the structure of the crystalline variety from which it was formed.¹ True the changes are utterly unlike in the two cases, but it seems just possible that the same principle may underlie both of them. It must be confessed, however, that all such comparisons are on the face of them extraordinarily far-fetched, and they do not touch the fact that the process of development is not a simple change, but involves an immense number of co-ordinated changes directed to a common end. (iii) The feature of heredity which is certainly peculiar is that it enables the germs of different kinds of living beings, while they are essentially alike, to behave differently in circumstances which are essentially the same—that is to say, to increase their unlikeness out of all proportion to the unlikeness of their surroundings. It is a remarkable fact that not only are the germs of organisms always more alike than their adults, but in some cases the closest microscopical and chemical investigation will reveal only the smallest differences between the germs of animals whose adults are extremely unlike. And in most of these cases the conditions (of warmth, nourishment, etc.) in which the germs develop differ as little as the germs themselves. The most striking case of this close resemblance of the germs and their conditions of development in very different animals is to be found in mammals. It is not at present possible to conceive how the great differences between a man and a horse can be due to the small differences which can as yet be recognised between their ova. All this, of course, is not to deny that there is anything in the germs in question which brings about the differences in their adults. It is merely to assert that

¹ By melting and pouring into water.

the development of the living germ is directed in a way which is as yet incomprehensible and cannot be paralleled in lifeless matter. In heredity, then, we find that reproduction does present a property peculiar to living beings.

6. It will be seen, however, that this property is of a directive nature. That is to say, it is a manifestation of that *purposiveness* which we have already seen to govern all the activities of living beings, and to be peculiar to them.

We may sum up the foregoing considerations as follows.

Summary. The possibly peculiar features of the living being are of two kinds. Some of the processes which constitute life—assimilation, conduction, and so forth—seem at present to involve capabilities which cannot be explained by the action of the forms of energy which are found in lifeless matter. On the other hand, all the life processes, whether they involve such capabilities or not, are peculiar in that they exhibit direction towards the welfare of the bodies in which they occur. Of this direction the processes of development, both in reproduction and in regeneration, are a special case. We have said that the body is a machine. We must now recognise that it differs from all other machines (1) possibly in possessing powers not found elsewhere, (2) in that its activity is directed to its own preservation and to that of its kind. In the present state of knowledge the division between living things and lifeless ones is wide and clear. If each of the processes of life could be paralleled in things which are not alive, it would still be necessary to explain how these processes came to be connected and directed as they are in living beings.

Two warnings, however, must be given lest the nature of these differences be misunderstood. It must in the first place be recognised clearly that the powers we have mentioned do not dispense the bodily machine from the obligation to act, like other machines, in conformity with the principle of the conservation of energy. What they appear to do is to enable it to effect *kinds* of transformation of energy which are not met with elsewhere. Like a steam-engine, the body can do nothing except in virtue of the energy which it obtains, in the long-run, from the food which becomes its fuel.

A Qualification.

It would appear, however, that, unlike the steam-engine, living bodies can use their energy in ways which are not possible outside themselves. Secondly, in the purposiveness of the processes of life we have a phenomenon, remarkable indeed, but not necessarily incapable of explanation.

So far we have been dealing with matters of fact. The existence in living beings of the peculiarities we have just stated is indisputable. Over their explanation, however, rages the great controversy of Biology. The *mechanistic* school of biologists regards all the phenomena of life as due to the laws of physics and chemistry, and looks forward to the day when the extension of our knowledge will enable us to explain them all in terms of these sciences. The apparent exceptions to the laws of chemistry and physics are, for it, not real exceptions, but are due only to our ignorance of the details of the processes in which they occur. The purposive direction of the life processes is due to the structure of the living machine, though here again our ignorance does not allow us to see how it is brought about. The *vitalistic* school believes that the present impossibility of understanding biological phenomena in the light of physical and chemical facts is due to the operation in living beings of a further factor or factors, without a knowledge of which life will never be explained. It is held that no machine can be conceived which would direct its own activity in the way in which the activity of a living being is directed. Indeed, the word "machine" can only be used in a limited sense of a living organism. As to the nature of this factor, if it exist, nothing is known, though there is a tendency among vitalists to regard it as psychical, but it must in any case be able to direct the physical and chemical forces of life without increasing or diminishing their energy.

The problem of the peculiarities of life is bound up with that of its origin. If we understood how life arose we should know to what its peculiarities are due, though it is true that we might well know this without being able to reproduce it. Life, as we have seen, is found only in

**Mechanism
and Vitalism.**

**The Origin of
Life: Organ-
ised Bodies.**

organised bodies, though not all organised bodies are alive. We may class material objects as follows:—

Organised	{	Living	}	Lifeless.
Unorganised		Dead		

It is possible that if we knew how organised bodies first arose we might understand the origin of life, but this is by no means certain. The organised body is one thing. The life in it is quite another. On this point cases of suspended vitality (p. 114) are an interesting commentary.

Organised bodies are characterised by peculiarities of structure, of composition, and of origin. Their peculiarities of structure and composition we have already studied. We may now consider their origin. Here we are met at the outset by a difficulty. We are bound to believe that these complex structures have arisen from matter in its simpler unorganised form.¹ The theories of special creation and of evolution agree in regarding the unorganised world as primary and organised bodies as derived from it. Yet organised bodies, alive or lifeless, never, in the present state of nature, arise from unorganised matter. Every such body arises by the process of fission from a previously existing living body. In the case of the higher organisms this is no more than a truism. We know that every individual of the familiar kinds of animals and plants had a parent from whose body it has arisen. But there are cases in which parentage is not so obvious. If the dead body of any organism be heated strongly, so as to kill any living things that may be in it, and placed in an apparently clean vessel, closed so as to prevent the entry of living organisms, it will nevertheless putrefy, and microscopical examination will show that putrefaction is accompanied by the appearance of innumerable

¹ It is true that the difficulty of conceiving how such a transition can have taken place has led certain authorities to the theory that life is coeval with matter, living substance being transferred through space from one celestial body to another—almost literally as a *deus ex machina*. Most biologists, however, are not content to give up the problem in this manner, though some are willing to admit that the earth may not have been the seat of the origin of life.

minute "micro-organisms" of various kinds (pp. 119, 127), some of which are indeed the cause of the putrefaction. Have not these been developed from the substance of the dead organism without the intervention of life? The answer to this question has not been easily reached. One of the hardest-fought controversies in the history of science has been between the supporters on the one hand of the theory of *Abiogenesis* or *Spontaneous Generation*—the origin of living from lifeless matter—and on the other of the rival and now victorious theory of *Biogenesis*, which maintains the aphorism *omne vivum e vivo*. Finally, however, it has been demonstrated that organic matter will not develop micro-organisms if, after being properly sterilised by heat, it be placed while it is still hot into a sterilised vessel to which only filtered air has access.¹ The explanation of the appearance of such organisms in other circumstances is that they give rise to minute germs or "spores" which are capable of existing in a dried state, and in that state are carried by the air to germinate when they fall on suitable ground. The micro-organisms are killed both in the organic matter and in the vessel by sterilisation, and their germs are filtered out from the air which enters as the vessel cools. In this, as in every other instance which has been carefully investigated, it is proved to be the case that organised bodies arise only from living bodies of their own kind. The first organised bodies must have arisen from unorganised matter, and it may be that the conditions in which this happened will some day be discovered and reproduced. But at present it is true that living organised bodies are necessary for the reproduction of their kind.

It will be seen that there are two distinct ways in which life is necessary for its own continued occurrence. It alone can provide the kind of body in which it occurs, and such a body cannot live unless the life of its parent be continued in it. Thus all life is part of a single, self-continued process. This, however, is no more than might be expected. If, as we

¹ The experiments are usually made with a broth or infusion of meat or hay which is kept in test tubes whose mouths are plugged with cotton wool, put in while the contents are boiling, to serve as a filter.

have seen to be the case, life requires substances which do not arise in lifeless nature and involves processes which lifeless things cannot carry out, it is not likely to arise spontaneously amid lifeless surroundings. It may well be that a process so peculiar required for its starting conditions which existed in a former state of the earth, but cannot now be reproduced. These conditions, whatever they may have been, must have included the presence of a factor that endowed the first living beings with some degree of that purposiveness without which they could not have survived. The circumstances which brought into being protoplasm in a state of metabolism must also have brought into being a rudimentary capacity for purposive reaction. It is interesting to speculate whether this could arise by a fortuitous arrangement of unorganised matter or must be regarded as the development of some latent tendency in the lifeless universe. In any case purposive reaction has evolved to greater complexity as living things themselves have evolved, and that presumably by variation and selection, if we accept this as the method of evolution of organisms. However that may be, the facts that we have here considered give a new importance to that ceaseless activity by which living beings maintain their existence amid their lifeless surroundings. If that activity failed or were overborne, life, so far as we can see, would cease for ever.

APPENDIX

PRACTICAL WORK

It is absolutely imperative that the student should make a careful personal examination of each of the animals about which he reads, and should verify to the utmost extent possible the statement made in his text-books. However clearly he may seem to have understood these statements he will never really comprehend any organism until he has handled it himself, nor will he by any other means realise that his subject-matter is the living animal and not what is said about it. In the following pages certain instructions are given to facilitate this practical work, but they must not be considered as exhaustive, and the student should follow out any lines of investigation which his own ingenuity can suggest to him.

The following apparatus, etc., will be needed :—

1. Some *dissecting instruments*, including two or three dissecting knives or *scalpels* of various sizes, a large and a small pair of *forceps*, a large and a small pair of fine-pointed dissecting *scissors*, a blunt probe or *seeker*, and some *needles* mounted in handles. A box of such instruments can be bought for about £1.
2. A *dissecting dish* for dissecting under water. A shallow pie-dish with a sheet of cork weighted with lead on the bottom will serve this purpose.
3. A *magnifying glass* with a stand and aim to hold it over the dish while both hands are used for dissection.
4. Some stout pins, a sponge, and a duster.
5. Some wide-mouthed jars with corks or stoppers to keep specimens for dissection or from day to day while they are being dissected. A 2 per cent. solution of formalin in water is the best preserving fluid in most cases, but 70 per cent. methylated spirit may be used.
6. Plenty of clean water.
7. Chloroform for killing, and various other reagents for staining, etc., which will be mentioned later.
8. A microscope with the apparatus and reagents necessary for its use (see p. 450).

In all cases in which it is possible, the animal should be *examined alive* before dissecting, staining, etc. The shape and attitudes, movements, method of feeding, respiratory movements, and so forth, should

be carefully noted. It must then be *killed* for detailed examination, which will generally include both dissection and microscope work. Small animals may be killed with a drop of some poisonous fluid, such as alcohol, or solutions of corrosive sublimate or osmic acid (see below). Cray-fishes are best killed by sudden immersion for a few seconds in boiling water. For most other animals the best method is the use of chloroform, either by placing them in a closed vessel with a bit of sponge soaked in the liquid, or by holding a cloth similarly soaked over the nostrils. Care should be taken that the exposure is long enough to kill.

Dissection is an art that must be acquired by practice. The following rules will be of use to the beginner. —

Dissection.

1. *Never start till you are sure what you are looking for.*
2. *Never cut anything till you know what it is*
3. *Fasten down the animal with pins to the bottom of the dissecting dish or with nails to a dissecting board (according to size) and keep the organs well stretched.*
4. *Dissect along, not across, such structures as nerves and blood vessels.*
5. *Keep your dissecting instruments sharp.* They should be scrupulously cleaned and dried before being put away, and fine instruments should never be used for coarse work.
6. Small animals, including the frog, should be dissected under water, which should be changed as soon as it becomes cloudy from the presence of blood, etc.

Careful *drawings* should be made at all stages of the examination. They should never be copied from books or lecture diagrams. The use of coloured chalks in these drawings is not desirable, as it enables you to represent an organ by a mass of colour without realising its outline. The drawings should be of a good size in order to show detail clearly. It is easier to draw a symmetrical object after making a faint line upon the paper for the middle of the object.

The use of a compound *microscope* also requires practice. Such a microscope consists of a *stand* bearing a horizontal *stage* for the object, a *mirror* to throw light through the object from below by way of a hole in the stage, a *diaphragm* to vary the amount of light, a vertical *tube* through which the object is viewed from above, and combinations of *lenses* which are placed at the ends of the tube. Two such combinations must be used—an *objective* or *object glass* which screws into the lower end of the tube, and an *ocular* or *eye-piece* which slips into the upper end. Objectives and oculars are of various powers, and an objective of high power may be used with an eye-piece of low power, or *vice versa*. The object is placed upon the stage and brought into focus by raising and lowering the tube. *Coarse adjustment* is effected by sliding the tube, either directly or by a rack and pinion, *fine adjustment* by raising or lowering the arm which holds the tube. This is done by a screw which works against a concealed spring. With the high power the objective is closer to the object, when it is in focus, than with the low. An object may be viewed either by *reflected light* falling upon it from above,

or, if it be transparent, by *transmitted light* cast through it from below by the mirror. The object is placed or *mounted* upon a glass *slide*. Usually it is immersed in some medium which is either temporarily or permanently fluid (see below). In this case it must be protected by a *coverslip* of thin glass.

In many cases it is desirable to stain the object. A few reagents, such as *methylene blue*, will stain living objects; for most **Staining** it is necessary that the animal or tissue should be killed. This is done with a *fixing agent*, a strong poison that kills rapidly and so allows the minimum of change to take place in the object. Saturated solution of *corrosive sublimate* in water, 2 per cent. solution of *osmic acid* in water, 1 per cent. solution of *glacial acetic acid* in water, *absolute alcohol*, and other substances, are used for this purpose. Osmic acid is useful for small animals; for tissues, a mixture of nine parts corrosive sublimate solution and one part glacial acetic acid is a good reagent. The specimen must be thoroughly washed to rid it of all traces of the fixative before staining. *Carmine* and *logwood* or *hæmatoxylin* are common stains. Various preparations of each of these are in use for different purposes; they can be bought ready made, and directions for preparing and using them may be found in books, such as Marshall and Hurst's *Practical Zoology*. *Borax carmine* and *hæmatoxylin* are alcohol stains. *Picrocarmine* is a water stain containing picric acid. After staining, the object must be washed with water or dilute alcohol to remove the excess of stain.

Small aquatic animals may be mounted alive in water; parts of the tissues of larger animals which are to be examined in the **Mounting.** living condition must be mounted in *normal salt solution*—a .75 per cent. solution of common salt in distilled water. This approximates more nearly to the natural fluids of the body, and has not the injurious effect of pure water. Objects which are intended for a prolonged examination should be mounted either in *glycerin* or in some solid medium, such as *glycerin jelly*, which becomes solid when cold, or *Canada balsam*, which becomes solid when dry. An object may be placed direct from water into glycerin; to be mounted in Canada balsam it must first be dehydrated by soaking in absolute alcohol, then steeped in *oil of cloves* or in *xylol* till the alcohol is removed, and then placed in a drop of balsam upon the slide and covered. The object should not be placed direct from water into absolute alcohol, lest the diffusion currents set up by this strong dehydrant should injure it, but 30, 50, 70, and 90 per cent. solutions of alcohol should be used successively for a period varying with the size and density of the object. Thus the complete process for staining and mounting in Canada balsam involves the successive use of: stain, 30 per cent. or 50 per cent. alcohol to wash, 70 per cent., 90 per cent., and absolute alcohol, xylol or oil of cloves, and Canada balsam. In the case of very small objects it is convenient to carry out these processes upon the slide, but they are generally performed in *watch glasses*.

It is often important to study slices or *sections* of animals, organs, or tissues. This may sometimes be done by placing the object (after *hardening* in absolute alcohol, corrosive sublimate, or other hardening agent) between two pieces of pith or carrot, and slicing off sections

freehand with a sharp razor. More often, however, it is necessary to use a section-cutting machine or *microtome*. The object is embedded before cutting in some fluid which solidifies, such as paraffin wax. The technique of this process should be learnt in the laboratory. It is described in Marshall and Hurst's *Practical Zoology* and other books.

The following hints will be of service in using the microscope :—

Hints on the use of the Microscope.

1. Examine every object first with the low power, using the high power afterwards if necessary.
2. Focus roughly with the coarse adjustment, and only then use the fine
3. Use the utmost care to prevent the objective from getting dirty. It is damaged by cleaning. Never use the high power without a cover glass. The eye-piece and objective may be cleaned if necessary with chamois leather or silk. Canada balsam may be removed by the *very* careful use of benzol or xylol, but in the laboratory it is better to leave this to the demonstrator.
4. The object may appear indistinct owing to the presence of dirt on the coverslip, the objective, or the ocular. If the dirt be upon the coverslip the dimness will be affected by moving the slide ; if it be upon the ocular, by turning the latter ; if neither of these be in fault the objective is dirty. In a wet preparation a dirty coverslip must be replaced ; a dry one may be cleaned in the same way as the objective.
5. If the tube will not slide freely, it or the inside of the collar tube which holds it is dirty. They may be cleaned by careful but vigorous rubbing with a dry duster.
6. Keep both eyes open in looking through the microscope.

The following is an outline of the procedure which should be followed in the practical examination of an animal :—

How to Examine an Animal.

1. Examine alive, as recommended above.
2. Make a drawing of the external features. These are generally best shown in a side view.
3. Make separate drawings of parts, such as limbs, the mouth, etc., which are not fully shown in your first drawing. In the case of the crayfish and cockroach this will involve several drawings of appendages.
4. If the animal have a perivisceral cavity in which the organs lie free, open this cavity and make a drawing of the organs *in situ* without disarrangement. Vertebrates should be opened on the ventral side, invertebrates on the dorsal. If the body wall be hard, as in the crayfish and cockroach, it may be removed as a single piece after two lateral incisions ; if it be soft, a median incision should be made, and the body wall turned back or *reflected* to each side and pinned out. In a vertebrate the skin and the muscular body wall should be turned over separately. The thorax of the rabbit should not be opened till a later stage, and the relation of the organs and cavities should be observed carefully during the process.
5. Remove the alimentary canal by cutting through its ends, and the mesentery if there be one. Draw (*a*) the removed canal,

- (b) the body cavity with the organs left behind. In the crayfish, the endophragmal skeleton must be cut away in order to show the nerve cord.
6. In a vertebrate, make a special dissection of the heart, the great vessels entering and leaving it, and the respiratory organs. Make a drawing.
 7. In a vertebrate, make a dissection of the organs of the neck and throat from the ventral side. Draw.
 8. Expose the brain or cerebral ganglia, and examine it *in situ* with its nerves. Draw. Remove, and draw dorsal and ventral views. Ninety per cent. alcohol is useful in whitening and hardening the nervous system.
 9. In a vertebrate, make a series of drawings of the parts of the skeleton. Skeletons may be prepared by removing most of the flesh and boiling or macerating (*i.e.* placing in water and allowing the flesh to rot). They should then be washed thoroughly and bleached in sunlight. Cartilaginous skeletons, however, should not be rotted or allowed to dry, but dipped into hot water for a few minutes and cleaned with a brush.
 10. Examine under a microscope: (a) some of the blood; (b) if possible the sperm; (c) in the case of at least one of the vertebrate animals, portions of the tissues fresh and stained; (d) in the case of small animals, transverse and longitudinal sections of the whole body.

The work of the student will be greatly facilitated by the use of a good manual of practical work. Among such books may

Books. be mentioned Marshall and Hurst's *Practical Zoology*, T. J. and W. N. Parker's *Practical Zoology*, T. J. Parker's *Zootomy*, Marshall's *The Frog*, and the *Notebooks* which are used in the Zoological Laboratory of the University of Cambridge.

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